PLANT SUCCESSION IN THE ARCTIC BROOKS RANGE: FLORISTIC PATTERNS FROM ALPINE TO FOOTHILLS, ALONG A GLACIAL CHRONOSEQUENCE AND ELEVATION GRADIENT

By

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Abstract

In the wake of rapid glacial retreat, alpine habitats in the arctic are expanding as freshly exposed surfaces become vegetated. Many glaciers in alpine cirques have nearly disappeared, and little is known about the rate of colonization or pioneer communities that develop following deglaciation. Newly developed habitats may provide refugia for sensitive arctic flora and fauna, especially in light of polar warming. To assess this process, vegetation communities developing on two recently deglaciated moraines in the Central Brooks Range were surveyed and compared with communities along a transect spanning both a glacial chronosequence (40-125,000 years since deglaciation) and an elevation gradient (1700-500 m) into the Arctic foothills. Results show that primary succession begins almost immediately following deglaciation. Within forty years fine-grained and rock substrates hosted small communities of 8-13 vascular and non-vascular plant species. Many pioneer taxa, especially lichens, persist into later stages of succession. Overall succession is directional and slow, increasing in species richness for about 10,000 years, after which richness decreases and communities stabilize. This is the first vegetation study on primary succession in the high Central Brooks Range, providing a missing link to a vegetation transect along the Arctic Bioclimatic gradient.

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not significant; p >0.05, z =-5.7, d.f. = 11). **Panel D:** mean freeze season (October-May) temperature (temperature differences between Atigun Pass and Imnavait creek are not significant; p >0.05, z =-1.5, d.f. = 11). All r^2 values are not statistically significant (p >0.05, t = -1.3, d.f. = 11).

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Statement by Author

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Introduction

The Brooks Range, an Arctic mountain range extending some 1000 km from the Chukchi Sea to the Alaska/Yukon border, presently separates boreal forest to its south from tundra to its north. The Brooks Range has been repeatedly glaciated over the last several million years, and glaciers have deposited numerous moraines and other glacial landforms that are now vegetated. The glaciers remaining in the highest peaks of the Brooks Range have been retreating rapidly over the last several centuries, since the end of the Little Ice Age (LIA), and most are now reduced into high cirques (Figure 1) (Ellis 1978; Pendleton et al. 2015). As these small glaciers disappear and new surfaces are exposed, fresh substrate becomes available for colonization by pioneer plant communities during primary succession. Rapid, recent glacial retreat in the central Brooks Range creates an ideal setting to study the patterns and processes of primary succession in an arctic-alpine environment.

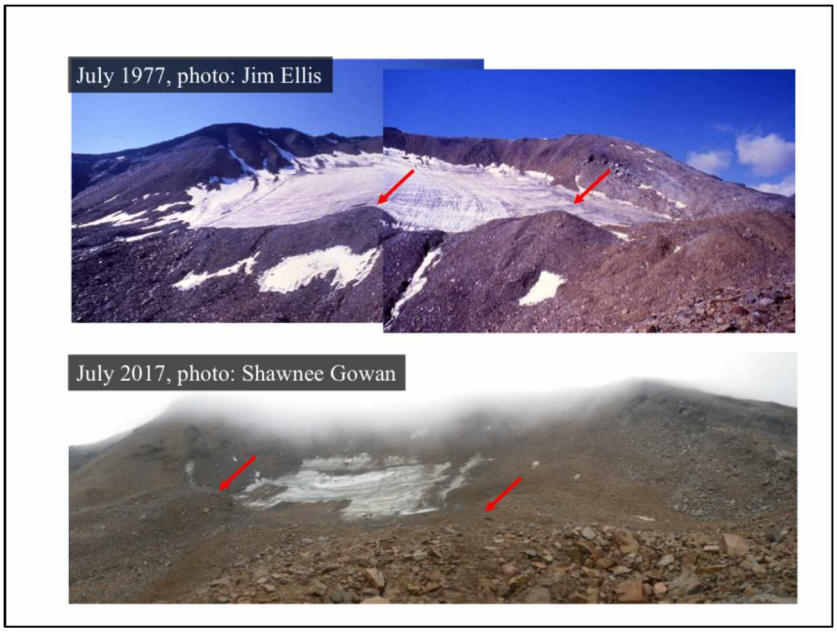

Figure 1. (above) Grizzly Glacier cirque photographed by Jim Ellis in July of 1977. **(below)** The same general scene photographed by the author in July, 2017. Note, these photographs were taken from slightly different distances and locations from the glacier. Red arrows indicate moraine features for comparison of ice mass.

In contrast to the extensive studies of primary succession that have been carried out at lower latitudes, little is known about processes of plant succession in Arctic mountain ranges, despite the fact that these environments are now on the front line of rapid climate changes. Primary succession affects the process of soil development, alters nutrient cycling, and plant communities formed during this process become the foundations of ecological communities. Hence changes in vegetation have the potential to create new habitats, accommodate the shifting ranges of animal taxa, and determine biodiversity. In the rapidly changing Arctic, understanding the trajectories and rates of these ecological changes could help us predict and manage the ecological impacts of ongoing climate changes and other disturbances.

Retreating glaciers in the central Brooks Range have left behind a complex mosaic of different substrates ranging from boulder fields to scattered pockets of fine-grained sediment. Course-grained habitats possess a relatively harsh microclimate that is ideal for only a small suite of plants to colonize (e.g., crustose lichens). Fine-grained habitats are more hospitable to a broader range of plants which require deeper soils with increased nutrient and water availability for root establishment. These two habitat types occur on glacial deposits of all ages and at all altitudes (Figure 2), from the crest of the Brooks Range to the foothills abutting the northern slopes.

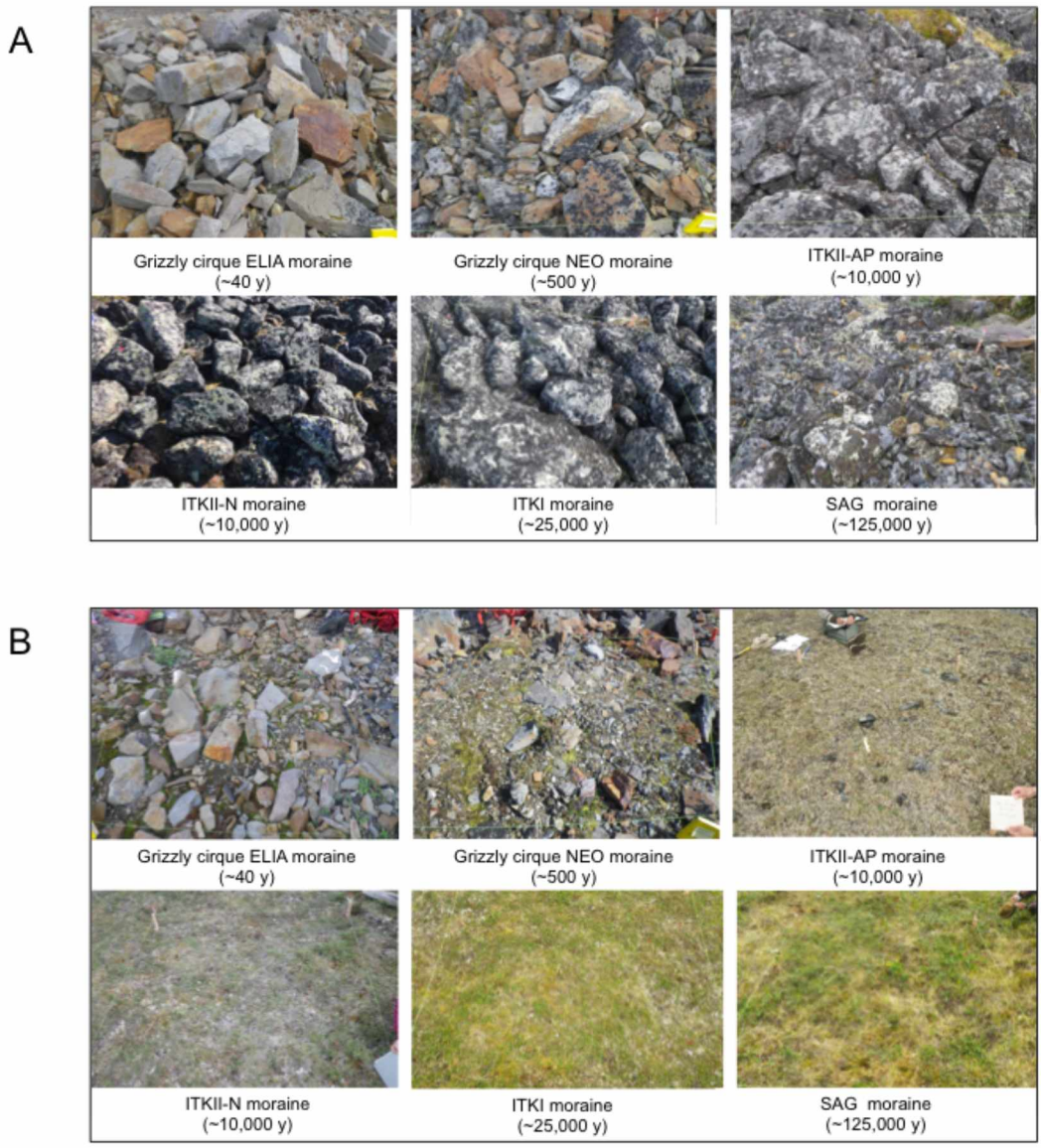

Figure 2. Examples of **(A)** rock and **(B)** fine-grained substrate relevés on each glacial deposit surface in order of the estimated age since deglaciation. For a full set of plot photos see Appendix A.

Arctic environments are inherently more harsh than those at lower latitudes due to colder climate, shorter growing seasons, and generally lower soil fertility (e.g., Svoboda & Henry 1987; Olech et al. 2011). Most arctic plants are adapted to these conditions and are vulnerable to interspecific competition and slight environmental change (see review in Vowles & Björk 2019).

In harsh environments, where inter-specific competition is generally reduced, colonizing plants tend to facilitate later successional plants. Early successional species facilitate later successional species by increasing available nutrients and creating more hospitable microclimate conditions (Svoboda & Henry 1987; Chapin et al. 1994; Callaway & Walker 1997; Anthelme et al. 2014; Reid et al. 2015).

At low altitudes in the Arctic, habitats on even slightly raised topographic features (e.g., moraines, kames & pingos), can reflect plant communities found in the alpine. For example, many of these communities are dominated by non-vascular plants such as lichens and bryophytes (Olech et al. 2011), whereas lowland communities at lower latitudes tend to be dominated by vascular plant growth forms (Chapin et al. 1994; Lang et al. 2012). Certain plant growth forms are commonly found in both Arctic and Arctic-alpine habitats, but are less common at lower latitudes such as plants that grow in low cushions or mats. This growth form allows for facilitation of neighboring species as well as self-proliferation by increasing soil accumulation, nutrient availability and regulating microclimate conditions (Reid et al. 2015). Therefore, along an Arctic glacial chronosequence and elevation gradient, the effect of altitude on plant community formation may be buffered by distinct environmental similarities between lowland and alpine sites.

Globally, the Arctic is at the forefront of climate change impacts, which are particularly amplified by loss of sea ice in the Arctic Ocean (Hinzman et al. 2005; Wendler et al. 2010; Bhatt et al. 2010). However, the impacts and severity of climate change vary across Arctic regions, and warming is having more drastic impacts on plant communities at lower altitudes. This is due in part to direct effects on frozen ground containing ice-rich permafrost (e.g., thermokarsting and cryoturbation; Olech et al. 2011; Walker et al. 2015), which is less common in the arctic-alpine,

than in tundra communities at lower altitudes. Low altitude sites are also more impacted by the expansion of shrubs (shrubification) across the tundra, which is limited in the arctic-alpine by environmental conditions such as cooler and shorter growing seasons, lower soil quality, and generally less substrate stability (Cornelissen et al. 2001; Lang et al. 2012; Vowles & Björk 2019). Anthropogenic disturbance (e.g., road construction & infrastructure development) is also more common at lower elevations, often reducing or changing habitat, resulting in similar impacts on vegetation communities as warming such as increased flooding, alteration of microtopography, and loss of organic layer (Walker et al. 2015) . Differences between alpine and lowland environments in the Arctic will likely result in warming under current conditions to be beneficial to alpine communities by causing alpine vegetation to proliferate and increase in floral biodiversity, and harmful to lowland communities causing a loss in habitat and floristic diversity (Carlson et al. 2014). Identifying rates and patterns of community development during primary succession in the arctic-alpine is important for understanding how communities respond to change. Contrasting early successional plant communities with plant communities on similar substrates at lower altitudes is important for predicting how young communities will develop over time, and what environmental factors drive development.

By comparing the present-day vegetation on two common habitat types across a glacial chronosequence and elevation gradient, I assessed the effects of altitude, time, and environment on the nature of plant communities and the trajectory of succession. This research is based on two main goals focusing on primary succession in the arctic-alpine and successional processes over the course of 125,000 years and 900m in altitude: 1.) document community development of new alpine habitat in a recently deglaciated cirque. 2.) use older glacial deposits at varying elevations to form an understanding of how pioneer plant communities develop over time.

These goals were substantiated by addressing two major objectives: 1.) determine what plant species are pioneer colonizers, what communities they form and at what general pace colonization takes place. 2.) determine how long plant communities undergo succession along this transect, how communities change, and what major environmental factors drive these changes.

Background

Study Area and Geology

The Brooks Range is part of the physiographic division known as the Arctic Mountains province consisting of mountains and hills generally around 2,000 m above sea level (a.s.l.) carved from Paleozoic and Mesozoic sedimentary rocks (Wahrhaftig 1965). Underlying bedrock in the Brooks Range is composed chiefly of Paleozoic (345-600 million years) limestone, shale, quartzite, slate and schist, with granitic intrusions in some of the higher regions (Wahrhaftig 1965). The Atigun Pass area is a complex mixture of highly resistant Kanayut Conglomerate, sandstone, shale, and limestone (Ellis 1978; Mull & Adams 1989) and includes the glacial deposits that were analyzed as the alpine relevés in this study.

The Arctic Foothills province is divided into the northern and southern foothills. The southern foothills are between 370 and 1070 m above sea level, characterized by irregular buttes, knobs, mesas, and east-trending ridges intervening with undulating tundra plains (Wahrhaftig 1965). They are underlain by diverse sedimentary rocks of Devonian to Cretaceous age with mafic intrusions (Wahrhaftig 1965). These Southern foothills (hereafter referred to as "foothills") abut the northern slope of the Central Brooks Range and include the glacial deposits that were analyzed as the lowland relevé locations in this study.

Glacial history

During the Pleistocene, large valley glaciers developed in the Brooks Range (Wahrhaftig 1965). The grinding action of these glaciers enlarged valley heads into cirques and steepened mountainsides leaving jagged ridges (arêtes) and spires (Wahrhaftig 1965). Three major glacial advances occurred in the central Brooks Range during the last 200,000 years: the Sagavanirktok River (SAG; 125,000-150,000 yr), the Itkillik I (ITKI; 50,000-70,000 yr), and the Itkillik II (ITKII; 10,000-25,000 yr) (Table 1, Figure 3; Hamilton & Porter 1975; Ellis 1978). All three of these advances involved valley glaciers descending out of the Brooks Range into the adjacent foothills where they deposited sweeping moraine systems and extensive outwash terrains below 800 m. After retreating into high cirques during the early Holocene (ca. 11,000-8000 years ago), glaciers underwent a series of minor Neoglacial re-advances starting ca. 4000 years ago that deposited prominent end moraines in cirques above 1800 m a.s.l.. The final Neoglacial advances of cirque glaciers took place during the Little Ice Age (LIA) (ca. AD 1250-1850). Little Ice Age advances left end moraines located inside those deposited during their maximum Neoglacial advances (Hamilton & Porter 1975; Ellis 1978).

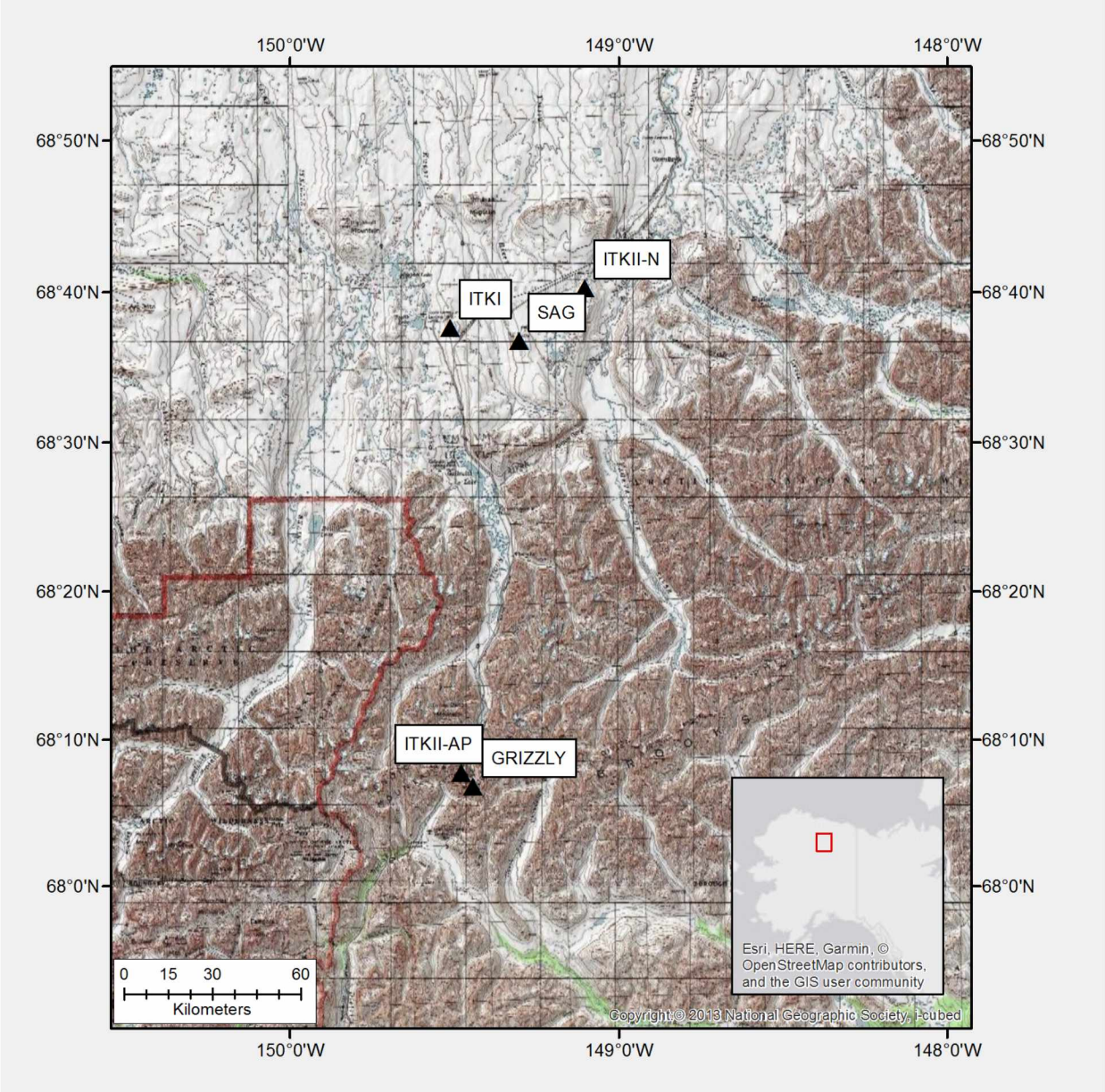

Figure 3. Study site locations. From youngest to oldest; the Grizzly Glacier site includes the End of Little Ice Age moraine (ELIA) and the Neoglacial moraine (NEO), Itkillik II aged glacial deposits are located at Atigun Pass (ITKII-AP) and near the toe of Slope Mountain in the foothills (ITKII-N), the Itkillik I moraine (ITKI) and Sagavanirktok moraine (SAG) are located between Imnavait Creek and Toolik lake in the foothills.

Table 1. Study site characteristics, and relevés sampled per site.

Glacial deposit	Average Elevation (M)	Latitude and Longitude (DD)	Estimated Age (Years BP)	Rock Relevés (N)	Fine-Grained Relevés (N)
End of Little Ice Age (ELIA)	1700	68.1133 N, 149.4426 W	40-100	3	3
Neoglacial (NEO)	1700	68.1132 N, 149.4386 W	500-1,000	3	3
Itkillik II Alpine (ITKII-AP)	1500	68.1299 N, 149.4770 W	10,000-15,000	4	4
Itkillik II Foothills (ITKII-N)	800	68.6762 N, 149.0888 W	10,000-15,000	5	5
Itkillik I (ITKI)	900	68. 8672 N, 149.5101 W	25,000-75,000	3	3
Sagavanirktok (SAG)	950	68.6125 N, 149.30016 W	125,000-150,000	3	3
(N relevés=42)	**Δ altitude = 750 *m***		**Δ time = 149,900 *years***	**N=21**	**N=21**

Regardless of their ages and altitudes, glacial deposits all contained patches of both fine-grained sediment consisting mainly of sand and silt, and coarse-grained sediment dominated by

boulders (Figure 2). These differences in sediment texture persist for hundreds of thousands of years in the Arctic where physical weathering is a slow process (Hudec 1973; Chen et al. 2000). They impose important legacies on the vegetation cover because both substrate and microclimate can limit the establishment of pioneer species. For example, the porosity of a surface determines which species can establish their rhizoids, hyphae, or rooting systems (Chen et al. 2000; Mori et al. 2013). Also, the texture of soil determines water retention capacities and space available for root colonization (Robbins & Matthews 2009; Mori et al. 2013), the color of a surface influences the heat flux of a given area, and the amount of microtopography available influences exposure levels and the catchment of fine-grained materials, detritus, spores, and seeds (Robbins & Matthews 2009; Mori et al. 2013).

Climate

Weather stations established by the Army Core of Engineers Cold Regions Research and Engineering Lab (CRREL) since the development of the Dalton Highway in the late 1970s (Haugen & Brown 1970; Haugen 1982), are currently monitored by the Natural Resource Conservation Service and have been maintained at multiple locations along the highway. These stations provide some historical record of climatic variation over a variety of time frames since the 1980s. However, much of this data is spotty until around 2006, and therefore provide only a little more than a decade of consistent temperature and precipitation data. There are long term climate records from Toolik Lake and Imnavait Creek dating back to the 1980s, but these data were unobtainable for this study outside of publicly available resources (e.g., Cherry et al.2014 in Hobbie & Kling; Haugen 1982)

Although other parts of the Alaskan Arctic have shown pronounced warming trends and associated impacts (e.g., Jia et al. 2003; Hinzman et al. 2005; Wendler et al. 2010),

climatic warming has not recently (e.g., since the 1980s) been pronounced in the central Brooks Range or in the southern foothills (Cherry et al. 2014 in Hobbie & Kling; Figure 4). However, based on the CRREL weather stations located in the mountains at Atigun Pass (SNOTEL #957), and at Imnavait Creek in the foothills (SNOTEL #968), some weak changes in temperature trends can be observed (Figure 4; $r^2<0.35$, $p>0.05$, d.f. = 11). For example, the most distinct temperature trend over the last decade for the study area is an overall decrease in average growing season temperatures of about 4ºC. Growing season temperatures are also significantly different between alpine and foothill sites (Figure 4A; $p<0.05$, $z=28.8$, d.f. = 11). Additionally, summer Warmth Index (SWI), the sum of all mean monthly temperatures > 0ºC, is decreasing across the area, more so in the mountains than in the foothills (Figure 4B). Satellite data for Western North America also shows a steady decline in SWI since 1998 (Bhatt et al. 2013), demonstrating that this trend has been ongoing for longer than this decade-long record.

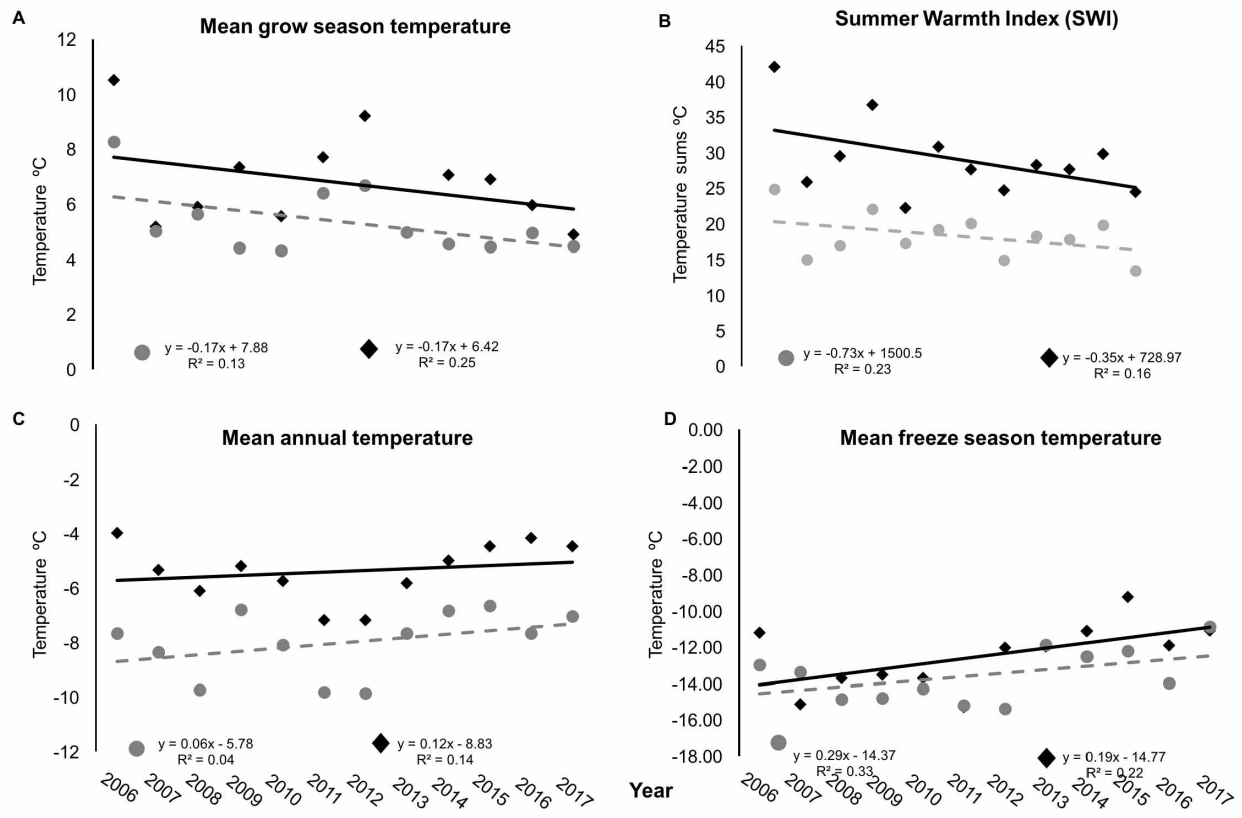

Figure 4. Climate trends from the alpine at Atigun Pass (SNOTEL #957 **grey circles**) and the foothills at Imnavait Creek (SNOTEL #968**, black diamonds**) weather stations for 2006-2018. **Panel A**: mean grow season (June-September) temperature (temperature differences between Atigun Pass and Imnavait creek are significant; **p <0.05, z =28.8, d.f. = 11**). **Panel B:** Summer Warmth Index (SWI), the sum of all average monthly temperatures > 0 °C in a given year (temperature differences between Atigun Pass and Imnavait creek are not significant; p >0.05, z =5.9. **Panel C:** mean annual temperatures (temperature differences between Atigun Pass and Imnavait creek are not significant; p >0.05, z =-5.7, d.f. = 11). **Panel D:** mean freeze season (October-May) temperature (temperature differences between Atigun Pass and Imnavait creek are not significant; p >0.05, z =-1.5, d.f. = 11). All r^2 values are not statistically significant (p >0.05, t = -1.3, d.f. = 11).

Some short-term climatic trends show a weak temperature increase in the study area (Figure 4C & D). For example, mean annual temperatures are increasing slightly, more so in the foothills than in the mountains (Figure 4C), and mean freeze season temperatures are also increasing slightly, in this case, more so in the mountains than in the foothills (Figure 4D). However, the increase in freeze season temperatures is becoming more pronounced since

2013, especially in the foothills (Figure 4C). Additionally, snowpack and precipitation levels have been relatively unchanged in the foothills since the late 1980s (Cherry et al. 2014 in Hobbie & Kling). These confounding climatic variations and the importance of local vs extra-Arctic climate processes are current areas of high interest for Arctic ecologists working to better understand factors influencing vegetation change (Bhatt et al. 2010; Bhatt et al. 2013).

Differences in temperature between study sites in the foothills and the mountains, does generally place them into different bioclimatic subzones according to distinctions made in the Circumpolar Arctic Vegetation Map (CAVM) (CAVM Mapping Team et al. 2003). For example, according to the average summer warmth index, sites in the foothills fit into subzone E (mean growing season temperature 5-11°C; Figure 4A, SWI 22-42°C; Figure 4C), while the Arctic mountain sites fit into subzone D (mean growing season temperature 4-8°C; Figure 4A, SWI 12-25°C; Figure 4C; CAVM Mapping Team et al. 2003). Thus, these mild temperature differences between the two site elevations likely affect the vertical and horizontal structure of plant cover, species richness, dominant vegetation, and annual productivity (CAVM Mapping Team et al. 2003).

Vegetation

A wide variety of vegetation-oriented research has been conducted since the 1970s in the Arctic Foothills, north to the Beaufort Sea. Vegetation types of the foothills have been categorized and extensively mapped in this region (Walker et al. 1994; Walker & Walker 1996; Walker et al. 2016). Some vegetation data for alpine areas of the Brooks Range are available for the Arrigetch Peaks and the Arctic Parks (Cooper 1986; Jorgenson et al. 2009). However, much of the Alpine has yet to be surveyed, and very little is known about

new alpine communities forming in the glacial forelands being exposed in Brooks Range cirques. Despite this scarcity of vegetation surveys in the high alpine, habitat types similar to those surveyed here have been described floristically from block field and glacial erratic habitats near Imnavait creek and Toolik lake, and on pingo formations in the Arctic foothills (see Walker et al. 1994; Walker & Walker 1996). Many of the plant communities described on these formations from similar habitats closely resemble those identified here on rock and fine grained substrates at both high and low elevations.

Materials and methods

Study area, site selection and field sampling

This study utilizes a chronosequence consisting of six glacial deposits whose ages range from 40 to approximately 125,000 years since deglaciation (Table 1). These deposits are located along an altitudinal gradient extending from the peaks of the Brooks Range near Atigun Pass, north into the Southern Arctic Foothills (Figure 3). Study sites on these glacial deposits were accessed on foot and occasionally by helicopter from the Dalton Highway, and consisted of three alpine sites (ELIA, NEO, and ITKII-AP) near Atigun Pass, and three foothill sites north-east of Toolik Lake (ITKII-N, ITKI, SAG) (Figure 3). The two oldest glacial deposits only occur at the lowest altitudes in the foothills, and the two youngest glacial deposits only near the range crest. The only glacial deposits that occur in both the foothills and the alpine were deposited during the Itkillik II (ITKII) glaciation phase. Two study sites were established on glacial deposits of ITKII age to assess the effect of elevation on plant communities on glacial deposits of similar age — one near the summit of Atigun Pass (ITKII-AP; ~1500 m a.s.l.) and one in the foothills near Slope Mountain (ITKII-N; ~800 m a.s.l.; Figure 3).

Ecological and environmental data were collected from forty-two, 2-m x 2-m relevés. Three to five relevés were placed on both "rocky" deposits, and "fine-grained" sediments on each of the sampled glacial surfaces (Figure 2). "Fine-grained" relevés were placed on the crests of glacial deposits where boulders were scarce, well drained fine-grained sediment was abundant, and tussock vegetation was absent (Figure 2A). Corresponding "rocky" relevés were placed in areas dominated by well drained, large boulders with minimal bare soil (Figure 2B; see Appendix A for a full suite of plot photos). Plant communities were sampled in the field according to the Braun-Blanquet approach (Westhoff & Maarel 1978) as modified for Arctic plant-communities (Walker et al. 2016). Three to five permanent relevés were placed at random distances of at least 10 m from one another in representative areas along glacial deposit crests. Cover of each vascular plant, lichen, and bryophyte was visually estimated using Braun-Blanquet cover abundance scores (r = rare; + = common but <1%; 1 = 1–5%; 2 = 6–25%; 3 = 26–50%; 4 = 51–75%; 5 = 76–100%; Barkman et al. 1976, Supplementary material A). Relevés were established at least 1 km from the highway when possible on distinct glacial deposit ridges previously identified and dated (Calkin & Ellis 1980; Hamilton 2003). All sites were established in locations where siliceous rather than carbonate rock types are predominant.

Plant collection, curation and identification

Vascular plant collections were identified by the author with aid from Carolyn Parker, research professional at the University of Alaska Fairbanks Herbarium. Nomenclature for vascular plants and bryophytes follows the latest available edition of *Flora of North America* (1993+), and were synchronized with the Panarctic flora checklist when possible (http://panarcticflora.org/). Nomenclature for lichens follow the Consortium of North American Lichen Herbaria (lichenportal.org) and American Arctic Lichens Vol.1 & 2 (Thomson &

Brehmer 1984). Lichen species were identified by SK using standard chemical spot test and microscopy techniques, with verification aid provided by Dr. Mikhail P. Zhurbenko, lead researcher of the systematics and geography of fungi lab at the Komarov Botanical Institute Russian Academy of Sciences, and curated in the Komarov Botanical Institute non-vascular herbarium. Bryophyte collections were verified and curated by David Toren of the California Academy of Sciences Herbarium. A subset of bryophyte samples was verified by Andrew Cortese, M.Sc. at the University of Alaska Fairbanks, using standard microscopy techniques.

A representative sample of every plant species found on each relevé was collected for verification and comparison purposes whenever possible. Vascular plants were stored in a plant press while in the field, and cryptogams were stored either together by relevé or separately in labeled wax, paper, or plastic bags and allowed to air-dry. Voucher specimens of uncommon lichens and bryophytes were collected for herbaria curation. In the lab, plants were sorted, identified and given a collection number for further verification purposes.

Environmental data

A single temperature logging device ("ibutton" Maxim/Dallas Semiconductor Corp., Sunnyvale, CA, http://www.maxim-ic.com/) was placed in the southwest corner of each relevé just below the litter/moss layer of the soil to monitor soil-surface temperatures from August of 2017 through July of 2018. If the litter/moss layer was absent on a given relevé (e.g., on rock substrate), the ibutton was placed in a shallow depression and covered with a rock similar to those within the relevé at approximately the same depth. Using a combination of data gathered via ibuttons, and data from two weather stations located at Imnavait creek (SNOTEL #968) and at Atigun Pass (SNOTEL # 957) (National Water and Climate Conservation Staff), summer warmth index (SWI = the sum of mean monthly temperatures >0 °C), thawing-degree days and

freezing-degree days (sum of all positive (thawing) daily mean temperatures, and all negative (freezing) daily mean temperatures) were calculated. In the Grizzly Glacier cirque, one additional ibutton was placed just inside of the mouth of a PVC pipe approximately two meters above the ground surface and covered with duct tape to provide shade from the sun to compare ground and air temperatures.

When possible 235 cm^3 of soil, the volume of a standard soil can, was collected from just below the litter layer, to a depth of approximately 10 cm at the center of each relevé. These samples were analyzed for pH using a glass electrode pH meter and the paste method (McLean 1982). Moisture content was measured by comparing wet and dry weight of each sample for gravimetric soil moisture (Peters 1965), and when possible, volumetric soil moisture was also taken (Peters 1965). Soil particle size was analyzed by first sieving the soil through a 2 mm screen to remove gravel. Percent gravel was determined by subtracting the weight of the gravel removed via the sieve from the total dry weight of the soil sample. To determine percent sand, silt, and clay the hydrometer method was used (Bouyoucos 1962). Wet and dry soil color and chroma were determined using a Munsell color book (Munsell Color (Firm) 2009). Additionally, eighteen site characteristics (e.g. slope, aspect, elevation, landform, etc.) and percent cover of all plant growth forms, soil, rock and water were estimated and recorded for each plot in the field (See supplementary material A for a complete list of variables and categories assessed).

Lichenometry

Lichenometry is a widely used method for estimating the exposure age of rock surfaces based on the diameters of lichen thalli whose growth rates are known (Loso & Doak 2006; Wiles et al. 2010). Ellis & Calkin constructed a lichen-growth curve for the Central Brooks Range region (Figure 5), which they used to date the stabilization of the Neoglacial

(NEO) moraine in the Grizzly Glacier cirque in the late 1970s at approximately 500 years old. When a moraine is no longer shifting regularly due to ice melt both within the moraine and as the glacial terminus retreats, large rocks are no longer moving enough to prevent the colonization of lichens; this is when a moraine is considered to be stabilized for the purpose of this study. Following the methods of Ellis and Calkin (Calkin & Ellis 1980), lichenometry was used to estimate stabilization of the End of the Little Ice Age (ELIA) moraine and general rates of pioneer lichen colonization.

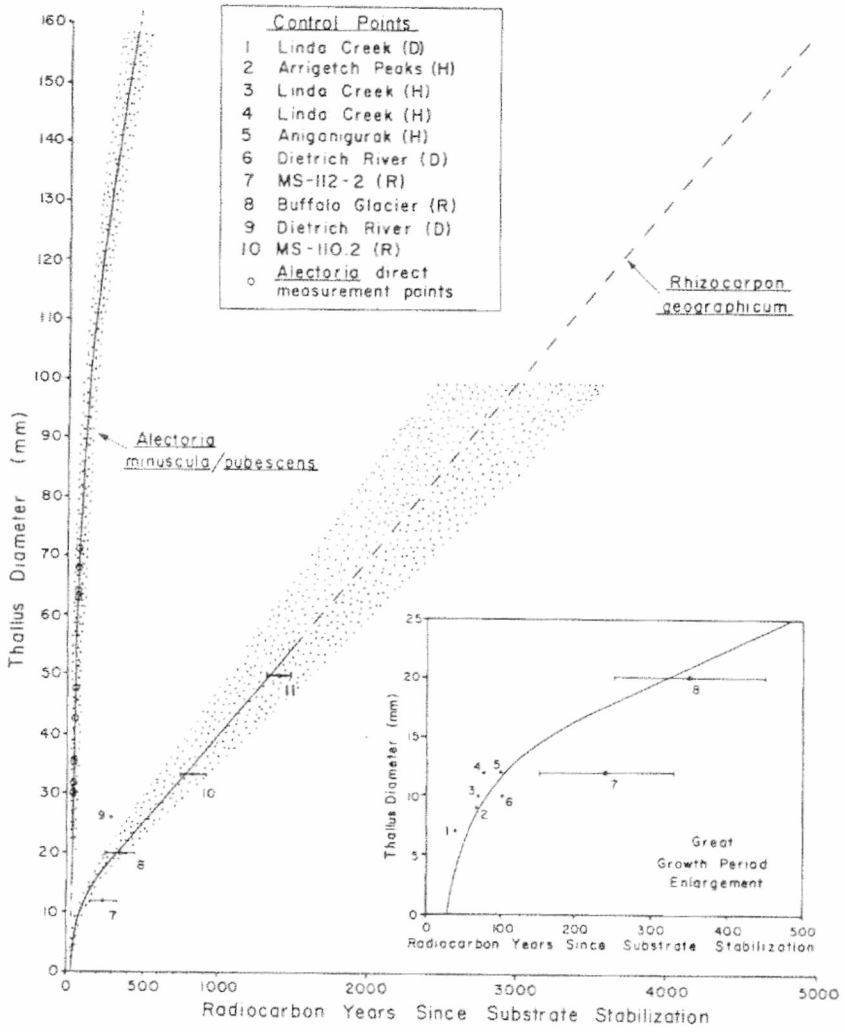

Figure 5. Lichen growth curves for the central Brooks Range showing the difference in growth rates between *Rhizocarpon geographicum*. and *Pseudephebe (Alectoria)* species. Figure adapted with permission from Jim Ellis (Ellis 1978; Calkin & Ellis 1980).

Rhizocarpon geographicum s.l. is an easily recognized saxicolous crust lichen most commonly used for this method (Webber & Andrews 1973; Calkin & Ellis 1980; Innes 1985; Wiles et al. 2010). It grows on a variety of rock substrates and environments, including the arctic-alpine. It should be noted that this lichen name consists of a complex of similar species, which have all been recorded to have similar growth rates in similar environments (Ellis 1978; Calkin & Ellis 1980; Innes 1985; Wiles et al. 2010), throughout this study it will be referred to singularly as *R. geographicum* s.l.. Other, faster growing species in the genera *Pseudephebe* (*P. minuscula* and *P. pubescens*) and *Umbilicaria* (*U. proboscidea*) are also used to date younger surfaces (Webber & Andrews 1973; Calkin & Ellis 1980; Calkin & Ellis 1980). These groups of species within the genera *Pseudephebe* and *Umbilicaria* have also been shown to share similar growth rates (Webber & Andrews 1973; Ellis 1978; Calkin & Ellis 1980), and will be discussed together as *Pseudephebe* and *Umbilicaria* spp. throughout. *R. geographicum* s.l. has been shown to grow at a rate of about 3 mm / 100 years in the central Brooks Range following a "great growth period" of about 200 years, during which *R. geographicum* s.l. goes from a growth rate of about 10 mm/ 100 years, slowing incrementally until stabilizing at about 3mm/ 100 years (Calkin & Ellis 1980; Figure 5). *Umbilicaria* spp. and *Pseudephebe* spp. grow about 7 x faster than *R. geographicum* and do not live as long as (hundreds vs. thousands of years) (Calkin & Ellis 1980; Figure 4).

The largest thalli of these lichen species were measured on multiple boulders on the Neoglacial (NEO) and End of Little Ice Age (ELIA) moraine in the Grizzly Glacier cirque. Age estimates were then made based on the lichenometric-age curve assembled for the central Brooks Range by Calkin and Ellis (Calkin & Ellis 1980) for *Pseudephebe* spp. and *R. geographicum* s.l.,

and colonization patterns were assessed based on the estimated age of the majority of the measured lichen thalli on each moraine. It should be noted that due to the small thallus size and lack of morphological distinction of *Umbilicaria* lichen thalli on the ELIA and NEO moraines, more than one *Umbilicaria* species (most likely: *U. hyperborea* & *U. cylindrica*) were included in this analysis, while only *U. proboscidea* has a known growth rate for the area. Despite this possibly confounding factor, *Umbilicaria* measurements of on both the ELIA and NEO moraines were generally consistent in maximum thallus size.

Data analysis

Data preparation

Two matrices of data were compiled for use in PC-ORD 7 (McCune & Mefford 2018) in Excel: (1) a species matrix containing relevé numbers (columns) and species names (rows) with Braun-Blanquet cover-abundance values in each cell (supplementary material B); (2) an environmental matrix containing plot numbers (columns) and environmental information (rows) (supplementary material A.)

Cluster analysis and synoptic table

The hierarchical dendrogram approach was used to assign relevés to discrete groups based on similarities in plant community composition. (PC-ORD 7 McCune & Mefford 2018) to create a dendrogram showing percent similarity between relevé communities. To obtain the most meaningful separation of all 42 relevés, Sørenson's distance measurement and a flexible beta group linkage method ($\beta = 0.25$) were selected as analytical parameters, identifying seven major clusters. Fidelity was defined by Phi correlation coefficients ranging from zero to one assigned via an indicator species analysis (Tichý 2002; PC-ORD 7 indicator species analysis tool, McCune & Mefford 2018). Species with phi coefficients ≥ 0.4 were considered somewhat

diagnostic, those with phi coefficients ≥ 0.5 were considered diagnostic and those with phi coefficients ≥ 0.8 were considered highly diagnostic. Since the phi value has no test of statistical significance associated with it (Chytrý et al. 2002), a Monte Carlo randomization test was used to assess if the phi values associated with each species within a cluster was less than 95% likely to have been assigned by chance ($p > 0.05$, 4999 randomized runs). A synoptic table was then prepared by hand, combining the results of the cluster analysis and the indicator species analysis. For each cluster in the synoptic table, diagnostic species were organized by fidelity (phi values from the indicator species analysis) from lowest to highest. The frequency of each species' occurrence in each cluster was determined by averaging species frequency across all relevés included in each cluster (Appendix B). Taxa that were non-diagnostic according to the indicator species analysis were removed from the clusters and included in the synoptic table section labeled: non-diagnostic taxa (Appendix B). Singly occurring species were removed from the clusters and included in the synoptic table section labeled: non-diagnostic singly occurring taxa (Appendix B).

Nonmetric Multidimensional Scaling ordination

The Non-Metric Multidimensional Scaling method (Kruskal 1964) provided a clear separation of communities in two-dimensional space across the chronosequence and elevation gradient and resulted in a relatively low-stress (10.4), three-dimensional solution with zero instability that accounted for the majority of the variability within the data ($r^2 = 0.84$), most of which was resolved in axis 1 and 2 ($r^2 = 0.65$). Plot and species similarities were calculated using Sørenson's distance measurement ($\beta = 0.25$) and run on "slow and thorough" in the autopilot setting within the PC-ORD 7 software (McCune & Mefford 2018). Relationships between plant species and environmental variables were visualized by both a bi-plot diagram highlighting

environmental variables that were relatively highly correlated to plant community separation ($r^2 \geq 0.3$) and the three NMS axes correlating to each environmental variable at each plot via Kendall's tau correlation coefficient. NMS axes were labeled with the most highly correlating environmental variables ($\tau \geq |0.5|$). Based on a 95% confidence interval, the significance of plant community groups identified in the ordination was tested using a multiple-rate permutation procedure (MRPP) analysis. Within group similarity was measured by the association coefficient (A value), which describes similarity within defined groups regardless of between group dissimilarity (McCune & Grace 2002).

Species richness and percent cover

To calculate species richness across the transect, the total number of species for each plant growth form (lichens, bryophytes, forbs, graminoids, shrubs, biological soil crust, and seedless vascular plants) were averaged from each glacial deposit on rock and fine-grained substrates separately. To calculate percent cover, field cover estimates for each plant growth form from each relevé were averaged from each glacial surface across the transect.

Results

Lichenometry

The maximum thallus size of *R. geographicum* s.l. lichens on the End of the Little Ice Age (ELIA) moraine measure 2-12mm in diameter, dating them between 20 to 40 years old, while the majority of those on the neoglacial (NEO) moraine were generally between 10-20mm in diameter, dating them between 300 and 700 years old (Figure 6). Based on these measurements, the ELIA moraine is estimated to have become mostly stabilized between 20 to 40 years ago, and measurements made on the NEO moraine are consistent with the date of stabilization estimated by Ellis (1978) of approximately 500 years since stabilization.

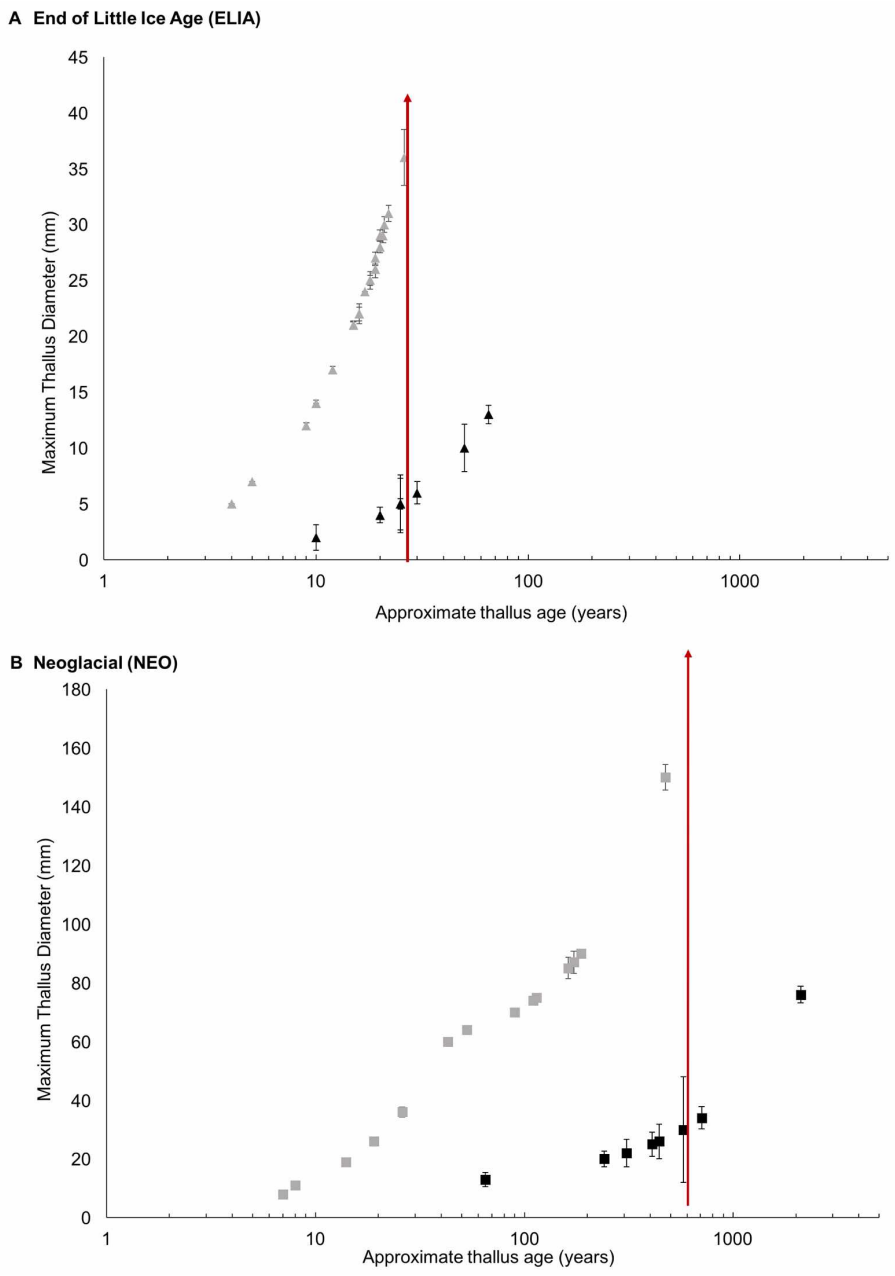

Figure 6. Maximum thallus radius measurements taken across both the End of Little Ice Age (**ELIA; panel A**) and Neoglacial (**NEO; panel B**) moraines in the Grizzly Glacier cirque from three different lichen taxa: *Rhizocarpon geographicum s.l.* (**shown in black**), *Pseudephebe* spp. and *Umbilicaria* spp. (**shown in grey**). Age estimates were derived from growth rates presented in Calkin and Ellis (1980). Error bars represent standard deviation. Red arrows indicate estimated stabilization time of each moraine.

The most common and widespread pioneer species on the ELIA moraine is *R. geographicum* s.l., followed by *Umbilicaria* spp. and then *Pseudephebe* spp., which are both less

abundant and frequent across the moraine (see supplementary material B). This identifies them as the earliest saxicolous pioneer species in the Grizzly Glacial cirque.

Cluster analysis and synoptic table

A list of all the vascular plants, lichens, and mosses and liverworts are in Appendix C. The species and environmental data from the plot surveys can be found in the supplementary materials (A & B). A dendrogram representing clusters of relevés that share similar plant communities was created using PC-ORD 7 (McCune & Mefford 2018; Figure 7). The synoptic table (Appendix B) shows all species occurring within each cluster, their frequency across all clusters, and diagnostic species for each cluster in order of descending fidelity (phi value). Fidelity is a statistical measurement of the concentration of species occurrences within vegetation units (Chytrý et al. 2002). The fidelity of a certain plant to a given community is measured by a phi value. The phi value ranges from 0-1 with values closer to 1 indicating a higher degree of fidelity (Chytrý et al. 2002). The clusters within the dendrogram are broken into three main subgroups of communities, defined by 1) successional state, 2) substrate type (rock/fine grain), and 3) elevation (alpine/foothills) (Figure 7). The main subgroups are broken into 7 main clusters of vegetation communities described below, with species listed in order of descending fidelity. In this classification, diagnostic species are commonly also the most abundant species within a given cluster. All environmental factors for each cluster and relevé can be found in supplementary material A, percent cover of growth forms on each relevé can be found for rock and fine-grain substrates on each glacial deposit in Appendix D.

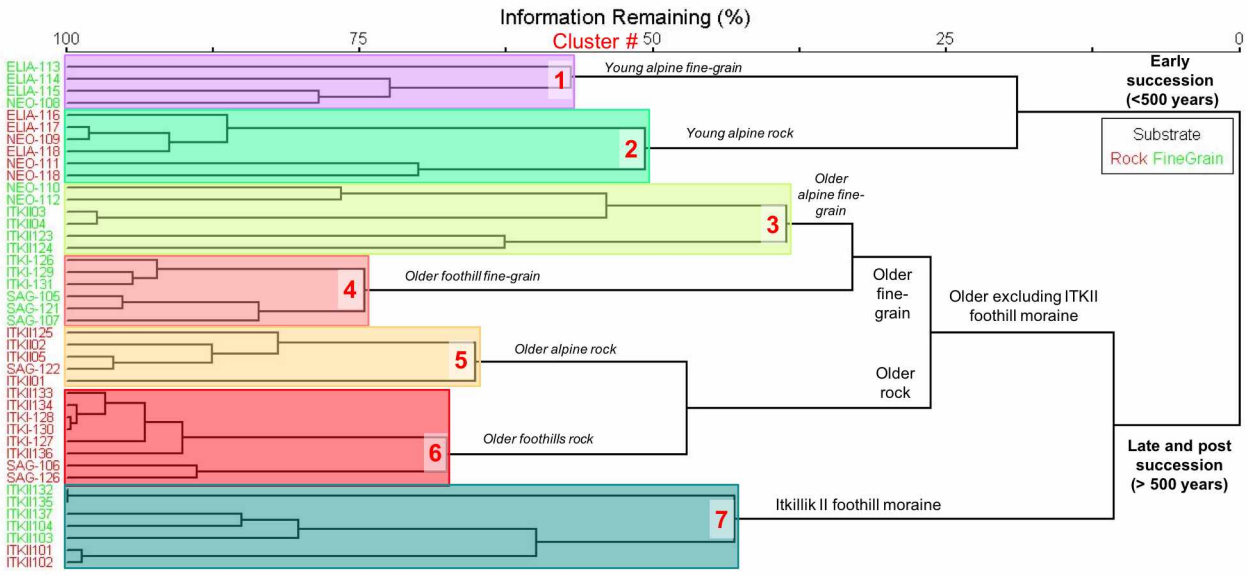

Figure 7. Cluster analysis of relevés. Study plot numbers are along the left axis with rocky-substrate plots (**red = rocky plots; green = fine-grained plots**). Seven main clusters of plots are defined by large red numbers and shading. Groups with highest percent floristic similarity are located closest to the left edge of the diagram, dissimilarity increases as subgroup nodes expand away from branch tips. Scale bar (top) shows percent similarity for each cluster.

Cluster 1: *Chamerion latifolium* & *Peltigera didactyla* community. This community contains all of the fine-grained ELIA relevés and one fine-grained NEO relevé, and is therefore an early-successional community. This is an alpine community located above 1700 m a.s.l. on well-drained, mesic moraine ridges. The soil is gravely and xeric (27% gravel, 12% moisture) with an average pH of 6.3. This community consists of a low shrub layer, an herbaceous layer and a cryptogam layer, averaging 7cm, 10cm, and 1cm, respectively. Total vegetation cover is around 9%, with high rock cover (70-90%) and is dominated by lichens and bryophytes.

This community has one very highly diagnostic species (phi $\geq$ 0.8, $p < 0.05$, mean phi = 0.25 ± s.d.0.10), the erect forb *Chamerion latifolium* (100% frequency), and three highly diagnostic species (phi $\geq$0.5, $p < 0.05$), the foliose lichen *Peltigera didactyla* (100% frequency, mean phi = 0.25 ± s.d. 0.10), the low shrub, *Salix arctica* (75% frequency, mean phi = 0.26 ± s.d. 0.11), and the foliose lichen *Peltigera venosa* (50% frequency, mean phi = 0.27± s.d. 0.12). This

cluster aligns closely with the class *Ceratodonto purpurei-Polytrichetea piliferi*; Mohan 1978 (in Mucina et al. 2016; p. 224), and within the alliance, *Peltigeretalia*; Klement 1949 (in Mucina et al. 2016; p. 225), or *Solorinion croceae*; Klement 1955 (in Mucina et al. 2016; p. 225). However, this class is described in Mucina (2016) by lichen communities only, and do not include two of the three dominant vascular taxa in the cluster, *C. latifolium* and *S. arctica.* The most abundant species in this cluster is the moss *Polytrichum juniperinum,* the lichen *P. didactyla*, and the forb *C. latifolium*. *P. juniperinum* is non-diagnostic and ubiquitous across glacial deposits.

Cluster 2: *Lecanora polytropa* & *Candellariella vitellina community.* This community contains all of the rock relevés in the Grizzly Glacier cirque on both the ELIA and NEO glacial deposits, and is therefore an early-successional community. This is an alpine community located above 1700 m a.s.l. on well-drained, mesic moraine ridge boulder fields. There is very little soil, which is xeric (18% gravel, 3-8% moisture) content between large boulders ranging in pH from 3-7. This community consists of a single cryptogam layer averaging 1cm in height. Total vegetation cover is between 29 and 37% on average and is dominated by crustose lichens.

This cluster has one very highly diagnostic species (phi ≥ 0.8, $p < 0.05$, mean phi = 0.25 ± s.d. 0.10), the crustose lichen *Lecanora polytropa* (100% frequency), and two highly diagnostic species (phi ≥ 0.5, $p < 0.05$), the crustose lichen *Candellariella vitellina* (frequency 100%, mean phi = 0.25 ± s.d. 0.10), and the foliose lichen *Umbilicaria cylindrica* (100% frequency, mean phi = 0.25 ± s.d. 0.10), all of which occur in 100% of relevés within this cluster. This cluster closely aligns with the class *Rhizocarpetea geographici*; Wirth 1972 (in Mucina et al. 2016; p. 224), and the alliance *Umbilicarion hirsutae*; Cernohorsky et Hadac in Smarda 1944 (in Mucina et al. 2016; p. 235).

Cluster 3: *Salix rotundifolia* & *Racomitrium lanuginosum* community. contains all fine grained relevés from alpine glacial deposits (above 1700 m a.s.l.), older than 40 years since deglaciation (NEO and ITKII-AP), and is thus beyond the pioneer stage of primary succession (500-125,000 years since deglaciation). This community is located on well-drained, xeric glacial deposit ridges. The soil is composed mostly of sand (37%) and gravel (25%) with an average pH of 3.5, and is also xeric (8% moisture). This community consists of a low shrub layer, an herbaceous layer and a cryptogam layer, averaging 0.5cm, 6.5cm, and 1cm, respectively. Total vegetation cover is around 68%, and is dominated by forbs and cryptogams.

This cluster has four highly diagnostic species (phi $\geq$ 0.5, $p < 0.05$), the dwarf shrub *Salix rotundifolia* (67% frequency, mean phi = 0.27 ± s.d. 0.11), the fruticose lichen *Dactylina ramulosa* (83% frequency, mean phi = 0.25 ± s.d. 0.1), the erect forb *Saxifraga cernua* (67% frequency, mean phi = 0.26 ± s.d. 0.11), and the erect forb *Draba macrocarpa* (50% frequency, mean phi = 0.27 ± s.d. 0.12). Two other species, the rush *Luzula confusa*, and the erect shrub *Saxifraga razshivinii* are highly diagnostic, but have insignificant phi values ($p > 0.05$, mean phi = 0.29 ± s.d. 0.10). Both of these species occur in 33% of relevés in this cluster. This cluster closely aligns with the alliance *Racomitrium lanuginose* in the class *Ceratodonto-polytrichetea*; Marstaller 2006 (in Mucina et al. 2016; p. 231). The most abundant species in this cluster are the lichens *Dactylina arctica, Cladonia arbuscula,* and *Cetraria ericetorum,* none of which are diagnostic species.

Cluster 4: *Betula nana* and *Masonhalea richardsonii community.* contains all fine-grained foothill (ITKI and SAG) relevés except for those on the ITKII-N moraine. This is a foothill community located between 900 and 950m a.s.l. on well-drained, mesic moraine ridges. The soil is moist (69%) with an average pH of 2.1, and is mostly composed of sand (51%) and

silt (21%). This community consists of a low shrub layer, an herbaceous layer and a cryptogam layer, averaging 4.5cm, 5cm, and 1cm, respectively. Total vegetation cover is highly stratified resulting in total cover greater than 100% (235%). This community is dominated by acrocarpous bryophytes, fruticose lichens, and shrubs.

This cluster has 11 highly diagnostic species (phi ≥ 0.5, $p < 0.05$), the low shrub *Cassiope tetragona* (67% frequency, mean phi = 0.27 ± s.d. 0.11), the foliose lichen *Masonhalea richardsonii* (100% frequency, mean phi = 0.25 ± s.d. 0.09) the low shrub *Vaccinium vitis-idaea* (83% frequency, mean phi = 0.26 ± s.d. 0.1), the fruticose lichen *Cladonia sulphurina* (100% frequency, mean phi = 0.25 ± s.d. 0.09), the dwarf shrub *Betula nana* (67% frequency, mean phi = 0.26 ± s.d. 0.1), the foliose lichen *Peltigera canina* (67% frequency, mean phi = 0.26 ± s.d. 0.1), the fruticose lichen *Cladonia bellidiflora* (50% frequency, mean phi = 0.27 ± s.d. 0.12), the cushion forb, *Diapensia lapponica* (50% frequency, mean phi = 0.27 ± s.d. 0.12), the erect forb *Polygonum bistorta* (50 % frequency, mean phi = 0.27 ± s.d. 0.11), the foliose lichen *Sticta arctica* (50% frequency, mean phi = 0.27 ± s.d. 0.12), and the grass *Poa alpina* (83% frequency, mean phi = 0.25 ± s.d. 0.10). This cluster most closely aligns with class *Loiseleurio procumbentis-Vaccinietea; Eggler* ex Schubert 1960 (in Mucina et al. 2016; p. 26). The most abundant species in this cluster are the low shrub, *Arctous alpina* and *Vaccinium vitis-idaea*, and the dwarf shrub *Betula nana*, however *A. alpina* is not a diagnostic species.

Cluster 5: *Porpidia flavocaerulescens, Cladonia squamosa* community. contains all older (> 500 years since deglaciation) alpine rock relevés, and one rock relevé from the oldest foothill (SAG) moraine. This is a mostly alpine community located above 1400 m a.s.l. on well-drained, mesic glacial deposit ridge block fields. Where soil is available between large boulders, it is moist (61%) with an average pH of 4 and is mostly composed of sand (46%) and silt (38%).

This community consists of a low shrub layer, an herbaceous layer and a cryptogam layer, averaging 0.5cm, 3cm, and 2cm, respectively. Total vegetation cover is around 102%, with overlapping lichen thalli. This community is dominated by lichens of all growth forms.

This cluster has seven highly diagnostic species (phi $\geq$ 0.5, $p < 0.05$), the foliose lichen *Cetraria nigricans* (60% frequency, mean phi = 0.27 ± s.d. 0.12), the rare crustose lichen, *Schaereria endocyanea* (40% frequency, mean phi = 0.29 ± s.d. 0.1), the moss *Schistidium apocarpum* (40% frequency, mean phi = 0.29 ± s.d. 0.10), the foliose lichen *Umbilicaria torrefecta* (40% frequency, mean phi = 0.29 ± s.d. 0.10), the crust lichen *Porpidia flavocaerulescens* (100% frequency, mean phi = 0.24 ± s.d. 0.09), the fruticose lichen, *Cladonia squamosa* (80% frequency, mean phi = 0.25 ± s.d. 0.1), and the moss *Tortella tortuosa* (60% frequency, mean phi = 0.26 ± s.d. 0.1). This cluster also most closely aligns with the class *Rhizocarpetea geographici*; Wirth 1972 (in Mucina et al. 2016; p. 224), and the alliance *Umbilicarion hirsutae*; Cernohorsky et Hadac in Smarda 1944 (in Mucina et al. 2016; p. 235). However, the overall community composition contains more graminoids than cluster 2 communities, and overall higher cover as this is a later-successional stage cluster. The most abundant species in this cluster are *Rhizocarpon geographicum*, *Umbilicaria hyperborea*, and *Rhizocarpon cinereovirens*.

Cluster 6: *Arctoparmelia centrifuga* & *Ophioparma lapponicum* community. contains all foothill (800-950m a.s.l.) rock relevés, with the exception of half of the ITKII-N rock relevés, and is thus a late-successional stage, foothill community. This community is located on well-drained, mesic glacial moraine-ridge block fields. Where soil is available between large boulders, it is moist (70%) with an average pH of 3 and is mostly composed of sand (86%) and gravel (28%). This community consists of a low shrub layer, an herbaceous layer and a

cryptogam layer, averaging 2.5cm, 4cm, and 1.5cm, respectively. Total vegetation cover is around 109%, with overlapping lichen thalli. This community is dominated by lichens of all growth forms.

This cluster has four highly diagnostic species (phi $\geq$ 0.5, $p < 0.05$), the crustose lichen *Ophioparma lapponica* (100% frequency, mean phi = 0.25 ± s.d. 0.1), the foliose lichen *Arctoparmelia centrifuga* (100% frequency, mean phi = 0.24 ± s.d. 0.09), the foliose lichen *Asahinea scholanderi* (50% frequency, mean phi = 0.27 ± s.d.0.11) and the crustose lichen *Rhizocarpon cinereovirens* (75% frequency, mean phi = 0.25 ± s.d. 0.10). This cluster aligns most closely with class *Rhizocarpetea geographici*; Wirth 1972 (in Mucina et al. 2016; p. 224) as well, but the alliance is unclear. The most abundant species in this cluster are *Arctoparmelia centrifuga, R. geographicum* and *U. hyperborea*, all of which are either highly or somewhat highly diagnostic of this cluster.

Cluster 7: *Mixed-plant-community cluster.* This is a foothill cluster located at approximately 800 m asl on a well-drained, mesic Itkillik II morainal ridge. It contains 2/5 of the rock relevés and all of the fine-grained relevés of the ITKII-N foothill moraine. This is the only cluster that has a combination of both rock and fine-grain relevés. The finer subgroup within this cluster separates the rock relevés on this moraine from fine-grain relevés, and thus this is likely a combination of two community types. The considerable heterogeneity within this cluster is likely a result of two main factors: (1) It was more difficult to find homogeneous groups of plots that corresponded to plots on other glacial sediments on this moraine compared to others in this study; (2) the moraine on which these plots were established is the result of a glacier that flowed down the Sagavanirktok River valley during the Itkillik II phase of glaciation. It could have carried limestone and other bedrock types that do not occur in the Grizzly Glacier cirque or the

headwaters of the Kuparuk River, where the other plots of the study are located. The soil is somewhat xeric (38% moisture) with an average pH of 3, and is mostly composed of sand (36%) and silt (23%) and gravel (27%). This community consists of a low shrub layer, an herbaceous layer and a cryptogam layer, averaging 7cm, 3cm, and 1cm, respectively. Total vegetation cover is about 95%, and is dominated by forbs and lichens.

Despite the likely combination of substrate types in this cluster, there is one very highly diagnostic species, the matt forb *Dryas integrifolia* (100% frequency, mean phi = 0.26 ± s.d. 0.10), and nine (phi $\geq$ 0.5, $p < 0.05$) highly diagnostic species, the foliose lichen *Hypogymnia austerodes* (100% frequency, mean phi = 0.25 ± s.d. 0.1), the erect forbs *Antennaria friesiana* (57% frequency, mean phi = 0.27 ± s.d. 0.12), *Oxytropis jordalii* (57 % frequency, mean phi = 0.27 ± 0.12), and *Pedicularis lanata* (57 % frequency, mean phi = 0.27 ± s.d. 0.11), the moss *Tomenthypnum nitens* (71 % frequency, mean phi = 0.26 ± s.d. 0.10), the crustose lichen *Ochrolechia upsaliensis* (43 % frequency, 0.27 ± s.d. 0.12), the erect forb *Bistorta vivipara* (57 % frequency, mean phi = 0.27 ± s.d. 0.11) the foliose lichen *Lobaria linita* (57 % frequency, mean phi = 0.27 ± 0.10) and the sedge *Kobresia myosuroides* (43% frequency, mean phi = 0.27 ± s.d. 0.11). Several of these taxa are diagnostic for previously described nonacidic vegetation types occurring in dry and mesic nonacidic habitats along floodplains of the Sagavanirktok River (Walker 1985; Schickhoff et al. 2002). Four highly diagnostic species have insignificant fidelity values ($p > 0.05$): the crustose lichen *Lecanora epibryon* (mean phi = 0.29 ± s.d. 0.10), the erect forb *Pedicularis capitata* (mean phi = 0.29 ± s.d. 0.1), the liverwort *Ptilidium ciliare* (mean phi = 0.29 ± s.d. 0.1), and the moss *Rhytidium rugosum* (mean phi = 0.29 ± s.d. 0.1), all occurring at a frequency of 29% in the cluster. This cluster most closely aligns with alliance *Dryadion integrifoliae*; Ohba ex Daniëls 1982 (in Mucina et al. 2016; p. 25), in class *Carici*

rupestris-Kobresietea bellardii; Ohba 1974 (in Mucina et al. 2016; p. 24). This class normally occurs on nonacidic substrates which is odd given the low pH of the sampled soils (pH 3-4). The most abundant species in this cluster are *Rhododendron lapponicum* and *Dryas integrifolia*, *R. lapponicum* is not a diagnostic species.

Nonmetric Multidimensional Scaling (NMS) ordination

The NMS ordination of all relevés along the chronosequence and altitudinal gradient (Figure 8), distributes relevés based on vegetation community similarity relative to environmental variation. The NMS ordination concluded with a three-dimensional solution explaining 84% of variation between communities after 75 iterations and a final ordination stress of 10.43. Axis one explained the majority of this variation (42 %), axis two explained 23 %, and axis three explained 19%. Since axis one and two explain the majority of the variation between communities, and correlate more strongly with environmental variables, these axes are the focus of this analysis. For a table of all environmental variables and correlation with each axis see Appendix E.

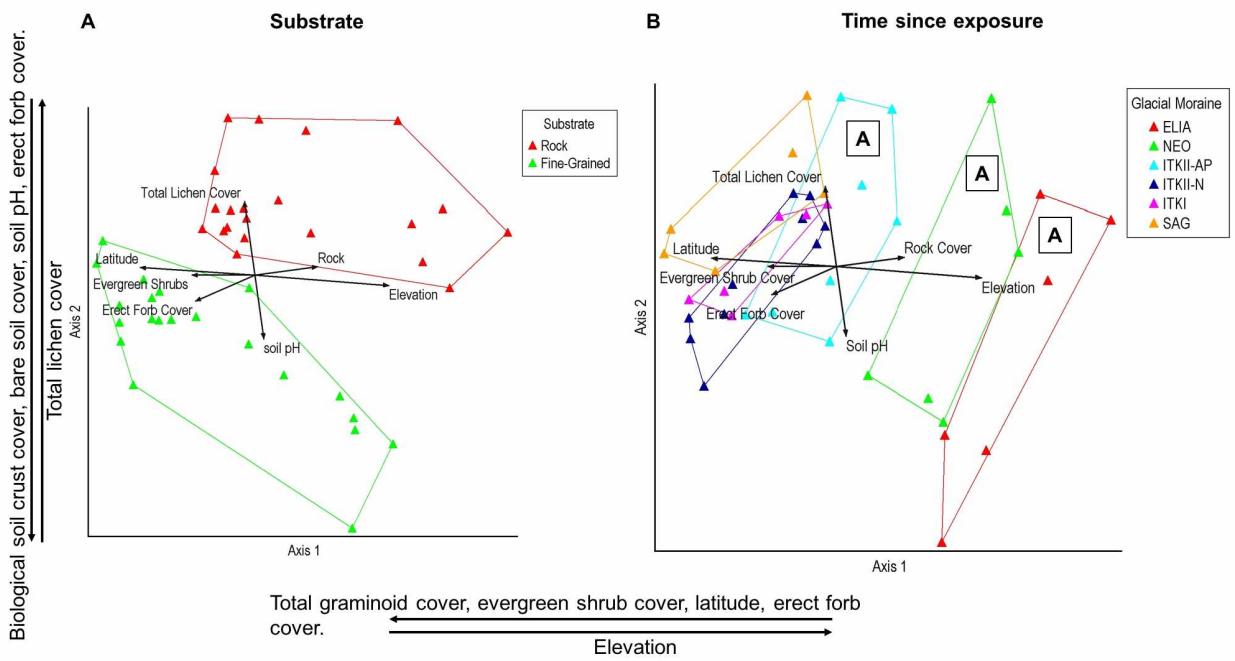

Figure 8. Nonmetric multidimensional scaling (NMS) ordination grouped by substrate **(A)** and time since exposure **(B).** Biplots within ordinations represent environmental factors with a Pearson's correlation coefficient $r^2 \geq 0.3$. Axes are determined by environmental factors with strong Kendall's tau ($\tau > 0.3$) correlation coefficients. Groups marked with **"A"** (**panel B**) indicate **alpine glacial deposits**.

Bi-plot diagrams within ordination space highlight the strongest linear environmental correlations with plant community variation ($r^2 \geq 0.3$; Figure 8). Biplots show that plant communities were separated first by substrate type (rock vs. fine-grain), with total lichen cover being highest on rock plots, distinguishing these from the fine-grain communities (biplot: r^2 >0.3). Fine grain communities were distinguished by shrub and forb cover, and lower soil pH (biplot: r^2>0.3). Environmental variables highly correlated with axes were determined by the Kendall's Tau correlation coefficient. Variables most strongly correlated with axis 1 (Kendall's Tau: $\tau > 0.5$) were total graminoid cover, evergreen shrub cover, elevation, latitude, and erect forb cover (Figure 8). The strongest correlation coefficients associated with axis 2 were less pronounced (Kendall's Tau: $0.4 > \tau < 0.5$) and include total lichen cover, biological soil crust cover, bare soil cover, soil pH, and erect forb cover.

Increased rock cover, higher elevation, and higher soil pH separate communities on the ELIA and NEO glacial deposits from older glacial deposits. Communities on the ITKII-AP alpine glacial deposit are the most similar to Grizzly Glacier cirque communities with respect to soil pH and rock cover, but are more similar to the foothill communities with respect to total lichen cover, shrub cover and forb cover. Sagavanirktok aged communities appear to be distinct from other foothill glacial deposits due to increased latitude and total lichen cover (Figure 8B). The multi-rate permutation procedure (MRPP) statistical analyses show that all groups are significantly different from each other based on time since deglaciation ($p < 0.05$, $t = -12.3$ d.f.= 5), and within group similarity (A) is relatively high: A= 0.15.

Species richness and percent cover

Plant species richness increases to a peak along the chronosequence on the ITKII foothill moraine (10,000 years since deglaciation) on fine-grained substrates and on rock substrates of the ITKI moraine (25,000 years since deglaciation), after which richness decreases (Figure 9, Table 2). There is not a significant difference ($p > 0.05$, $z = -0.8$, d.f. =11) in overall species richness between rock and fine-grained substrates across the entire chronosequence. However, there is a significant difference between species richness on rock and fine-grained substrates on both the ELIA moraine and on the ITKII alpine glacial deposit ($p < 0.05$; $z = -2.0$ & $z = -2.1$ respectively, d.f.= 5). There is no significant difference in species richness on either substrate on ITKII aged glacial deposits at low (ITKII-N) and high (ITKII-AP) elevations ($p > 0.05$; $z = 1.0$, $z = -1.7$ respectively, d.f. = 17) On rock, richness peaks at an average of 34 species, while on fine-grained substrates, richness peaks at an average of 36 species (Figure 9). After richness peaks, it declines through the end of the chronosequence at the SAG moraine (125,000 years since

deglaciation). Across all glacial deposits and substrates, the majority of species diversity are consistently found in the lichens (Figure 10).

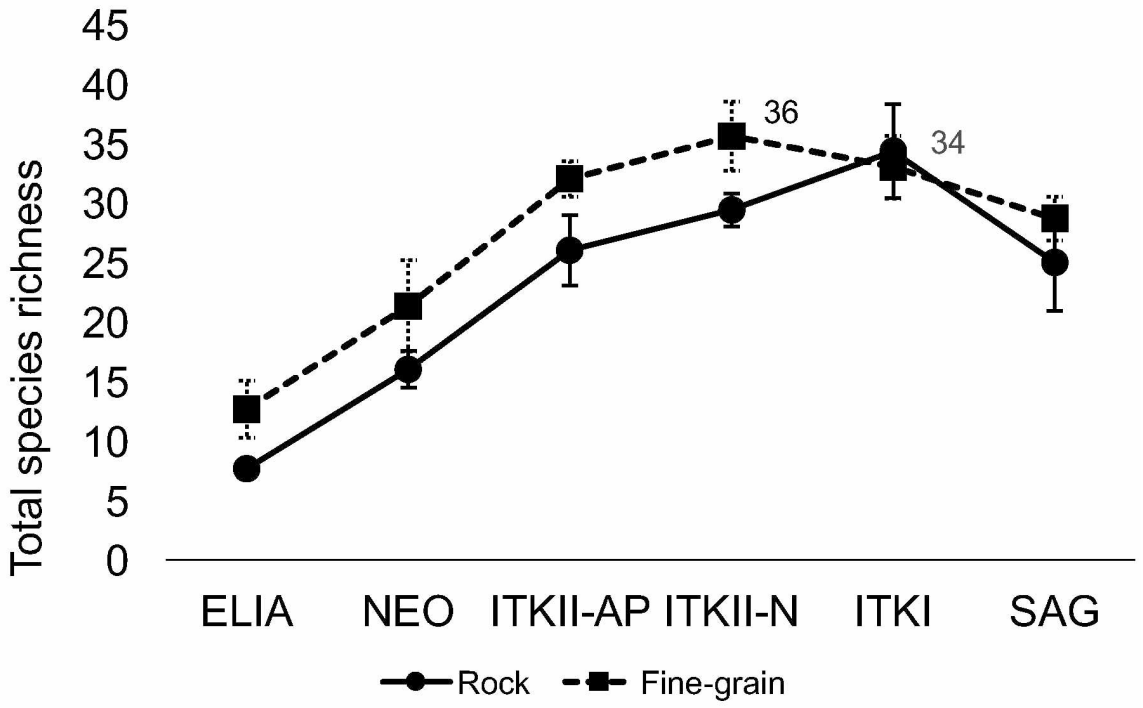

Figure 9. Species richness across glacial surfaces by substrate type (**rock:** solid line and circles, **fine-grain:** dashed line and squares). Error bars represent standard error.

Table 2. Percent change and number of plant species accumulated or lost from one glacial surface to the next across the chronosequence.

	ELIA to Neo Change in species diversity		Neo to ITKII-AP Change in species diversity		ITKII-AP to ITKII-N Change in species diversity		ITKII-N to ITKI Change in species diversity		ITKI to SAG Change in species diversity	
	Species percent change	Species accumulated / lost	Species percent change	Species accumulated / lost	Species percent change	Species accumulated / lost	Species percent change	Species accumulated / lost	Species percent change	Species accumulated / lost
Rock	56%	+10	38%	+11	15%	+5	15%	+6	-25%	-10
Fine grain	44%	+10	30%	+10	13%	+5	-6%	-2	-8%	-3

Representation of plant growth forms differs between substrate types (Figure 10 & 11). On rock substrates, graminoids do not appear until the ITKII surface, and are most abundant on the ITKII-N moraine (Figure 10A). Shrubs are only briefly represented on rock substrates starting on the ITKII alpine moraine, increasing in richness on the ITKII foothill moraine, and

decreasing throughout the rest of the chronosequence (Figure 10A). On fine-grained sites, lichens, bryophytes, forbs and shrubs are all represented on the youngest moraine (ELIA) and carry on throughout the chronosequence (Figure 10B). However, between the ELIA and NEO moraines, shrub richness decreases simultaneously with a pronounced increase in graminoid richness (Figure 10B). Between the NEO and ITKII alpine deposits, an increase in bryophyte and forb richness results in a decrease in graminoid and shrub richness (Figure 10B). On the ITKI and SAG moraines an increase in bryophyte richness accompanies a decrease in forb richness and vise-versa (Figure 10B). This variation in species richness by growth form shows minimal turnover, and incremental accumulation until reaching the two oldest glacial surfaces (ITKI & SAG).

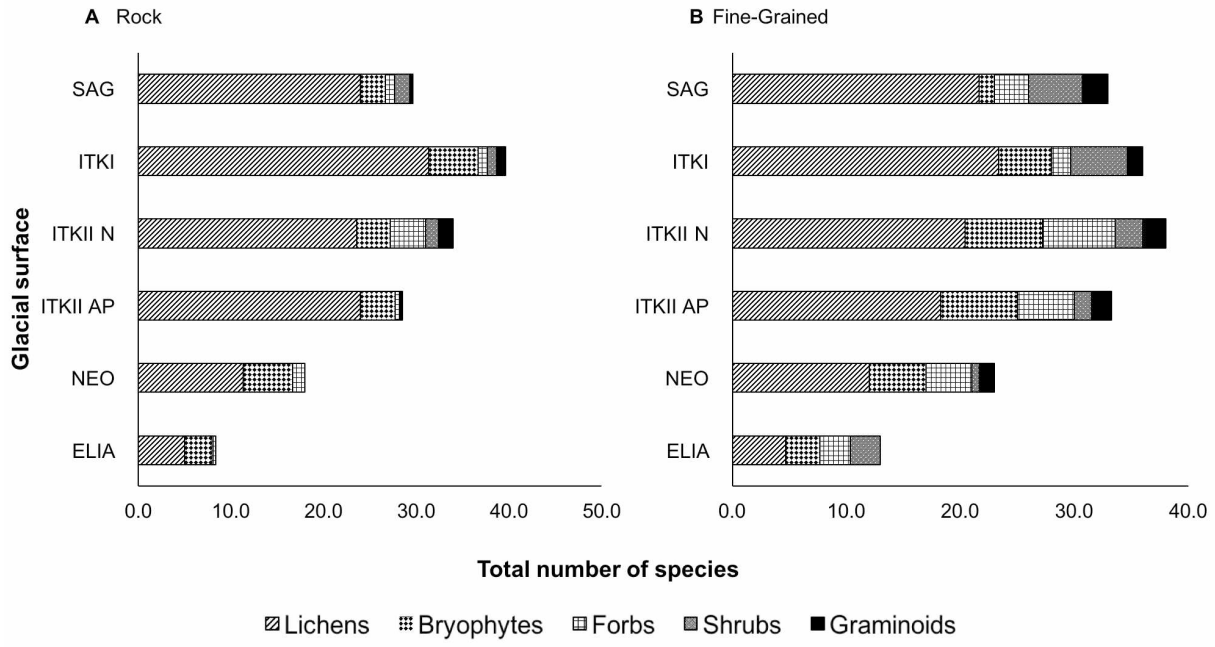

Figure 10. Species richness of each growth form (lichens, bryophytes, forbs, shrubs, and graminoids) on each glacial surface, separated by substrate **(rock: A, fine-grain: B).**

Average live vegetation cover increases and stratifies across the entire chronosequence on both substrates, reaching over 100% by the ITKII-AP moraine on rock substrates and the

ITKI moraine on fine-grained substrates (Figure 11). On rock sites, the majority of this cover is made up of lichens (Figure 11A), while on fine-grained lichens are most dominant on the ITKII alpine glacial deposit, and the ITKI and SAG moraines. On the ITKI and SAG moraines, lichen dominance is shared with shrubs, and bryophytes on the SAG moraine (Figure 11B). On rocky substrates, shrub cover peaks on the ITKI moraine, but is minimal on other glacial deposits (Figure 11A). On fine-grained sites, despite the higher diversity of shrubs on the ELIA moraine, shrub cover only makes up about 1% of the 8.5% of total average cover. Forb cover is small on all rock plots, peaking on the ITKII aged glacial deposits at high and low elevations. Graminoid cover increases between the NEO and ITKII-AP alpine glacial deposits on rock sites, decreasing to less than 1% of the total cover on other surfaces. On fine-grained sites graminoids cover follows a similar trend, increasing between the NEO and ITKII-AP glacial deposits and decreasing again until the SAG moraine where graminoid cover is maximized.

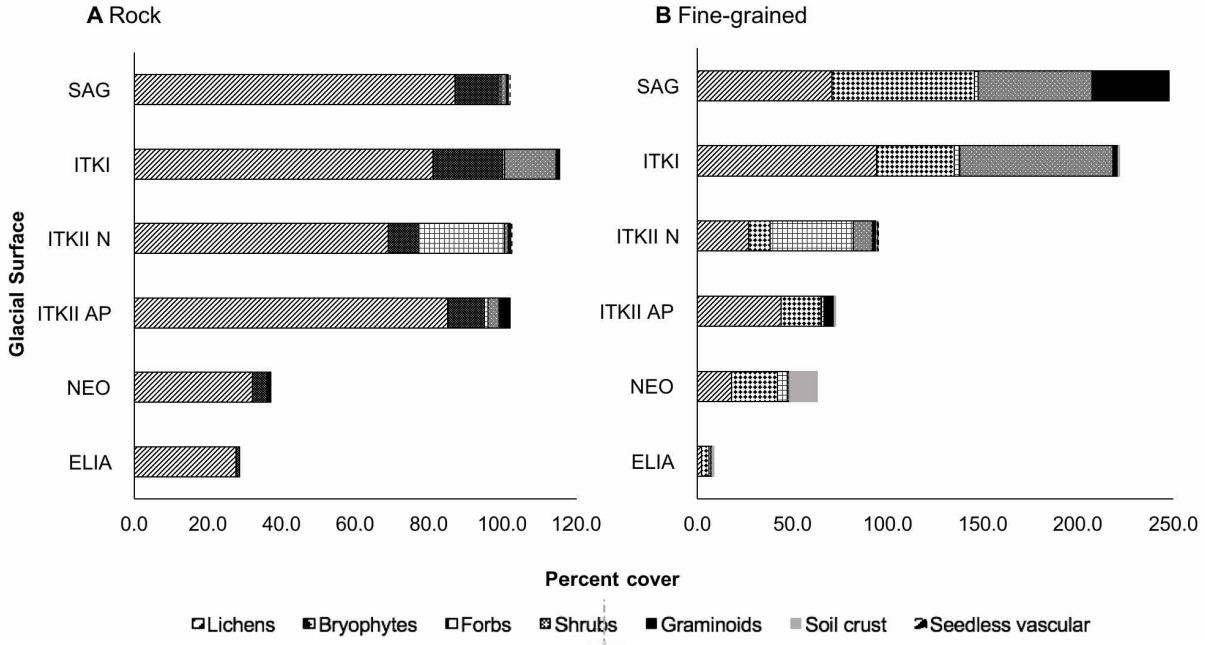

Figure 11. Percent cover of each growth form (lichens, bryophytes, forbs, shrubs, graminoids, soil crust, seedless vascular plants) on each glacial surface, separated by substrate **(rock: A, fine-grain: B).**

Pioneer communities

Both substrates on the ELIA moraine have few pioneer species on average (8-13) at low abundances (27% cover on rock and 8.5% cover on fine-grained sites; Figure 11, Appendix D). Pioneer vascular plant species do not persist abundantly throughout later stages of succession (e.g., the forb *C. latifolium* and the shrub *S. arctica*), however pioneer lichens and bryophytes more commonly do persist throughout later stages of succession (e.g., the lichen *P. didactyla* and the moss *P. juniperinum*). Pioneer species on rock substrates (e.g., *R. geographicum, and U. hyperborea*) especially tend to persist throughout succession and occur on all elevations along the sequence. The majority of diversity in colonizing species is made up of lichens on both substrates. Pioneer communities on rock substrates tend to primarily include lichens and bryophytes with the occasional forb (Figure 10 &11). Fine-grained sites are more diverse hosting approximately the same number of bryophyte, forb, and shrub pioneer species (Figure 10 &11).

Variation between alpine and foothill ITKII glacial deposits

When directly comparing plant community composition at low and high elevations on the ITKII glacial surfaces, species composition is comparable but dominant growth forms and taxa differ. Overall species richness increases by 15% from the alpine to the foothill ITKII surfaces (Figure 9, Table 2). Only 36% of species found on both substrates are shared across this elevation gradient, while 26% are unique to the alpine and 37% are unique to the foothill sites (see supplementary material B). Variation in total species richness between ITKII-AP and ITKII-N is equal on both rock and fine-grained substrates (Table 2). Specifically, alpine rock sites have a higher average percent cover of dwarf shrubs than foothill sites (3.5% vs. 1.5%; Figure 11A & Appendix D), while on fine-grained sites, the average percent cover of dwarf shrubs is almost 16-times higher in the foothills (10% vs. 0.5%; Figure 11B, Appendix D). Forbs make up

substantially more of the average overall cover on fine-grained foothill sites than in the alpine (54.5% vs. 1.25% respectively), but are relatively consistent across rock sites (Figure 11B, Appendix D).

Graminoids, lichens and bryophytes alike are more abundant on both substrates in the alpine than in the foothills. Cryptogamic growth forms vary noticeably between the low and high elevation ITKII surfaces. For example, on fine grained substrates foliose, fruticose, and crustose lichens are all more abundant in the alpine, whereas this is only true for fruticose lichens on rock sites (Figure 10&11). Pleurocarpous bryophytes are more abundant in the alpine across both substrates and acrocarpous bryophytes are more abundant in the alpine only on fine-grained sites.

Discussion

Successional timeline

40-500 years since deglaciation

Lichenometric measurements from the ELIA moraine indicate that this moraine stabilized between 20 and 30 years ago (Figure 6A). However, parts of the ELIA moraine still contain buried glacial ice, yet possess pioneer plant communities indistinguishable from surfaces that appear to lack remnant ice bodies; clearly then, moraines need not be free of ice (i.e. completely stabilized) before primary succession can commence (Figure 6A). The ELIA moraine was first colonized by the crustose lichen, *Rhizocarpon geographicum* s.l. shortly after glacial retreat and moraine stabilization (Figure 6A). Some of these *Rhizocarpon* individuals were probably "inherited" – individuals that survived transport on the glacier surface (Figure 6B). The estimated ages of *Umbilicaria* spp. and *Pseudephebe* spp. lichen thalli (3-30 years old on ELIA; 7-400 years old on NEO; Figure 6) suggests that these species began colonization after *R. geographicum* s.l. (10-70 years old on ELIA; 65-700 years old on NEO; Figure 6). These three

taxa were also the most abundant and frequent colonizers of rocky substrates on the youngest moraine (ELIA), and are thus the first three pioneer colonizers of this site. In addition to these three pioneer lichen taxa, the crustose lichens *L. polytropa* and *C. vitellina,* and the foliose lichen *U. cylindrica,* are less common but diagnostic species of early successional rock communities (Appendix B, cluster 2; Figure 12B).

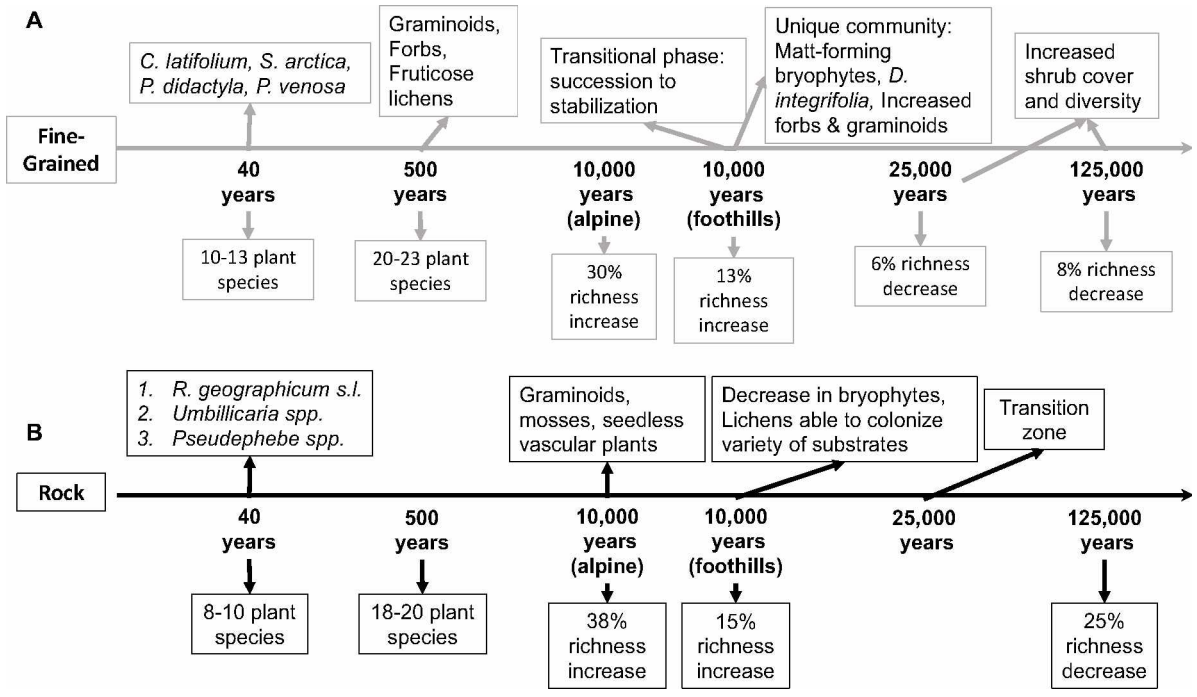

Figure 12. Timeline of major changes to vegetation communities on both fine-grained (**A**) and rock (**B**) substrates across a 125,000 year chronosequence and 750 m altitudinal gradient.

Primary succession on alpine cirque glacial deposits in the central Brooks Range begins within 10 years following deglaciation, with small communities of cryptogams and vascular plants assembling on both rock and fine-grained substrates within 40 years (Figure 6, Figure 12). Pioneer succession on fine-grained substrate is characterized by two vascular plants; the forb *C. latifolium* and the low shrub *S. arctica*. Both of these plants utilize aerial seed dispersal, giving them an advantage in accessing freshly exposed sites, and both species are known colonizers of

recently disturbed sites (Mori et al. 2013; Appendix B, Figure 12A). This pattern is consistent with another study in which these two dominated as pioneer species in the Arctic-alpine (Mori et al. 2013). This pioneer community is also characterized by two foliose lichen species, *P. didactyla* and *P. venosa,* both of which are symbiotic with cyanobacteria and fix atmospheric nitrogen (Thomson & Brehmer 1984; Appendix B, cluster 1; Figure 12A), giving them an advantage in colonizing nutrient-poor soils on freshly exposed surfaces.

500-10,000 years since deglaciation

Succession in this system is directional and slow. After 500 years of succession in the Grizzly glacial cirque, plant community size doubles on both fine-grained and rock substrates (Figure 9&12). Fine-grained communities begin to recruit graminoids, forbs, and fruticose lichens at this point in succession, and are generally more species rich and diverse in growth forms than rock communities throughout the chronosequence and elevation gradient transect (Figure 10 &11). Fine-grained sites continue to accumulate species for 10,000 years (ITKII), after which species diversity begins to decrease (Figure 9, 10, &12), and competition between plants likely increases.

In the foothills, the ITKII moraine (10,000 years since deglaciation) host plant communities that are unique in composition to all other glacial surfaces in the chrono-toposequence (See Appendix B, cluster 7; Figure 12). This moraine is where matt-forming bryophytes such as *Tomenthypnum nitens* become prevalent and forb and graminoid cover increases. Additionally, the most highly-diagnostic taxa for this group is an ectomycorrhizal forb, *Dryas integrifolia*, which may also fix atmospheric nitrogen (see Markham 2009). The unique community composition and competitive advantages of diagnostic taxa, combined with a loss of species richness, and increase in total vegetation cover following this phase, suggests that

the ITKII surface is the transitional point between plant communities still undergoing succession and accumulating species, and those beginning to stabilize and lose species richness. It may be inferred that this is also the transitional point between more facilitative interactions between plants towards more competitive interactions. However, it is possible that interactions between plants are not frequently occurring, rather than being facilitative up to this point in succession. Additionally, since glacial phases included in this study originate from separate alpine valleys, it is likely that substrate varies between sites more than has been detected here. For example, *D. integrifolia* and *T. nitens* are generally associated with calcareous substrates, but the average pH for the ITKII foothill moraine, where they are diagnostic, is between 3-4, which is acidic. It should be noted that this unique ITKII foothill community consists mostly of fine-grained relevés, but includes 2/5 rock relevés from this surface. The other 3 rock relevés from the ITKII foothill moraine were included in cluster 6, the foothill rock community (Appendix B, cluster 6, Figure 7). Therefore, cluster 7, or the unique ITKII foothill community is likely a combination of more than one plant community type. Nonetheless, results show that communities along this chrono-toposequence undergo succession for at least 10,000 years before beginning to stabilize.

25,000- 125,000 years since deglaciation

On rock substrates species accumulation continues for at least 25,000 years before richness decreases (Figure 9, 10, &12). At this point in succession graminoids, bryophytes, and seedless vascular plants become prevalent on rock communities (Figure 10, 11 &12). After 25,000 years (ITKI), fine-grained communities have decreased in richness by 6%, but increased in total vegetation cover by about 100% (Table 2, Figure 10B & 12A). Shrub cover and diversity begins to increase and continues to do so throughout the remainder of the chronosequence (125,000 years; SAG). On rock substrates, the ITKI glacial surface (25,000 years) is the most

species rich glacial surface (Figure 9&10) of the chronosequence. On this surface, forb and bryophyte cover in rock communities gives way to graminoid and shrub cover (Figure 11). Following this, rock species richness decreases by 25% on the SAG moraine, and fine-grained communities lose another 8% in richness (Table 2).

Overall, this sequence mimics a successional trend similar to other studies of alpine to sub-alpine systems (e.g., Matthews et al. 2018); a continuum from mostly self-replacement to mostly relay floristics as time since exposure increases. It should be noted that along a space-for time chronosequence other factors including seed and propagule rain affect species distribution (Chapin et al. 1994; Fastie 1995), so some instances of species turnover and high species accumulation may be in part the result of dispersal ability, seed banks of individual species, and their availability to different glacial deposits.

Species replacement across the chronosequence and elevational gradient

The Neoglacial moraine is about twice as species rich as the ELIA moraine (Figure 9&12) on both rock and fine grained substrates, illustrating the slow accumulation of species over 500 years in the high alpine. Interestingly, about 20% of the taxa on rock sites and 37% of species on fine-grained sites on the ELIA moraine are not found on NEO moraine relevés (supplementary material B). This demonstrates that the origin of pioneer colonizers is not only a matter of seed dispersal from nearby individuals, as the NEO glacial deposit is the only other substantially vegetated surface nearby. However, about 65% of pioneer (ELIA) species also occur in relevés on older glacial deposits, at various elevations on both substrates, illustrating low species replacement throughout the chronosequence and the ability of pioneer plants to tolerate conditions at both high and low elevations. Only 10%, of species on rock relevés and 17% on fine-grained relevés appear exclusively in the pioneer stage of succession, highlighting

the taxa most sensitive to competition in this sequence, and likely most specialized in pioneering freshly exposed substrate (Supplementary material B).

Plant communities on rock substrates are similar across all glacial deposits in the chronosequence and across the elevational gradient, and fit into the same vegetation class of *Rhizocarpetea geogrphici* (Mucina et al. 2016). These communities share many dominant species (e.g., *R. geographicum, U. cylindrica, U. hyperborea*) with older rock communities but generally become more species rich with increasing cover over time (Figure 10A, Figure 11A). For example, young alpine rock communities generally have more than 70% bare surface (Figure 11A) whereas older alpine and foothill rock communities tend to have >100% cover (Figure 11A). Bryophytes are more speciose in alpine rock communities (Figure 10A) than older foothill communities, but cover is highest on ITKII aged surfaces in the foothills (Figure 11A). In older foothill communities, bryophytes are replaced by a large diversity of lichens such as *Arctoparmelia centrifuga, Ophioparma lapponica,* and *Asahinea scholanderi*. This change shows that saxicolous bryophytes are likely better adapted to alpine environments while, larger foliose lichens, are better adapted to conditions at lower elevations. Additionally, more lichens that can grow on both soil and rock can be found on mature rock communities at lower elevations, (e.g., *A. scholanderi, Parmelia omphalodes*, and *Allocetraria madreporiformis*) showing how this flexibility in substrate preference likely comprises a competitive advantage.

All alpine fine-grain communities tentatively are placed into the same vegetation class, *Ceratodonto-polytrichetea*, but on older alpine glacial deposits forbs and graminoids become more abundant (Appendix B, cluster 1&3, Figure 10, 11, &12). Fine grained communities in the foothills and in the alpine share many of the same species but foothill communities have higher species richness and abundance of graminoids and shrubs on average (Figure 12A). For example,

cluster 4, which contains relevés on ITKI and SAG glacial deposits, is defined by low and dwarf shrubs (e.g., *C. tetragona, V. vitis-idaea* and *B. nana*) a variety of forbs (e.g., *D. lapponica, P. bistorta, and A. arctica*) and lichens that are both foliose (*M. richardsonii, F. cucullata*) and fruticose (*C. sulphurina, C. bellidiflora, C. acuminata*). Many of these species are not seen on alpine glacial deposits suggesting that either alpine conditions are limiting (e.g., the low shrubs *C. tetragona* and *V. vitis-idaea* and the lichens *C. sulphurina* and *C. bellidiflora* are acidophilus) and/or dispersal to high elevations is uncommon.

The proportional shifts in growth forms seen along this sequence illustrate which groups are most species rich across all surfaces, namely the lichens, which groups are more sensitive to alpine conditions, namely shrubs and graminoids, and which groups are more subject to turnover and presumably competition, namely forbs and bryophytes (Figure 10). Species richness of forbs and bryophytes decreased in response to increasing shrub and graminoid richness and cover (Figure 10). This shift suggests that these growth forms potentially compete with each other on older glacial deposits; when forbs are more speciose, bryophytes are more species poor and vice-versa. This is likely partially in response to microhabitat characters being slightly more favorable for bryophytes on the ITKI glacial deposit and more hospitable for forbs and graminoids on the SAG glacial deposit. Increased moss cover can make seed germination of some plants like forbs and graminoids more difficult, depending on the thickness of the moss layer, and high cover of forbs and grasses can prevent bryophytes from creating mats (e.g., Jeschke & Kiehl 2008).

Shrubs are likely the strongest competitors in this system and have the most potential to outcompete sensitive species (e.g., Cornelissen et al. 2001; Myers-Smith et al. 2011; Lang et al. 2012). Many shrubs are limited by certain environmental conditions such as soil quality and exposure, factors that are often poor in alpine habitats (e.g., Myers-Smith et al. 2011; Tape et al.

2012; Vowles & Björk 2019). For example, multiple dwarf and low shrub species are found in alpine habitats, but at low cover, and shrub cover is substantially higher on ITKII-N foothill glacial deposit than on the ITKII-AP alpine glacial deposit (11% vs 1%; Table 3). This demonstrates the shrub expansion potential in the alpine compared to the foothills is substantially smaller given current environmental conditions.

Glacial deposits with high species richness of one growth form doesn't necessarily translate to high abundance or cover. For example, on the SAG glacial deposit where bryophyte richness decreases, total bryophyte cover is highest relative to all other glacial deposits (Figures 10&11). Graminoids on fine grained surfaces are most speciose on ITKII surfaces but cover is highest on SAG surfaces (Figures 10&11). In general, high species richness of a given growth form does correlate with high cover of that growth form in this system. Instances in which species richness is low but cover is high highlights those species that have a competitive/adaptive advantage on a given substrate of a particular age (Figure 10&11, Appendix D).

Lichen induced weathering

Saxicolous (rock dwelling) cryptogams provide micro-topography that facilitates the catchment of fine-grained sediments and retention of moisture during early stages of succession, which in turn plays a role in the mechanical and chemical weathering of rock into soil (Chen et al. 2000; Ríos et al. 2002). However, the process of rock weathering appears to be particularly slow along this transect. For example, weathering rinds examined from lichen-colonized rocks of assorted lithologies from the oldest moraine surfaces (ITKI & SAG) were generally less than 1 mm thick, and very few fungal hyphae were visible under scanning electron microscopy. On glacial deposits younger than 25,000 years, little or no weathering rind could be seen, showing

that saxicolous lichens are contributing very little to soil accumulation via the weathering process along this chrono-toposequence. This seems to be due to a combination of harsh environmental conditions causing slow growth rates, and the extremely dense nature of the siliceous parent material (mostly Kanayut conglomerate) that serves as substrate for saxicolous organisms. However, superficial depressions on rock surfaces can allow for the catchment of fine-grained sediments and can be widened slightly by increasing plant biomass, allowing for a broader variety of plants to colonize (see review in Chen et al. 2000). Additionally, boulder fields tend to have more microtopography than fine-grained sites, allowing for soil and detritus to build up in depressions, eventually facilitating the root-systems of vascular plants such as the shrubs and graminoids that are seen becoming more common on older moraines in this study (SAG and ITKI; Figure 10A &11A).

The importance of symbiosis: why lichens prevail

Lichens are the most species rich growth form across the entire chronosequence on both substrates, and dominate some communities at both high and low elevations (Figure 10&11). They are also a major component of total vegetation cover across the chronosequence and elevation gradient, especially on rock substrates (Figure 11). This is somewhat counter to other studies which have shown a decrease in macrolichen richness and cover in response to increasing shrub, graminoid, and bryophyte cover (Cornelissen et al. 2001; Lang et al. 2012). There are more cryptogamic than vascular species, especially lichens, found on fine-grained substrates of the ELIA glacial deposit that are ubiquitous across all glacial surfaces (Appendix A&B). On rock substrates, dominant cryptogams can be found across all glacial deposits throughout the chrono-toposequence. This shows that cryptogamic pioneer species are more likely than vascular plant

species to persist in communities throughout succession, although many have cover values low (≤ 1%) within those communities. Thus, being symbiotic (e.g., lichens) is highly beneficial to colonizing freshly exposed substrates in harsh environments and persisting in and/or dominating communities at later stages of succession.

Environmental variation across the chronosequence and elevational gradient

Environmental factors, measured or estimated, that correlate most strongly with the separation of communities (Figure 8) are largely based on the percent cover of plant growth forms (biotic) rather than environmental differences (abiotic) between sites. Most of the environmental factors measured or estimated on each glacial deposit (e.g, slope, aspect, soil texture, stability, and moisture) were relatively similar and did not strongly correlate with the separation of plant communities on different glacial deposits, with the exception of soil pH (Figure 8). Soil pH was much higher (around 7) in alpine than in foothill sites (between 4 and 2). However, temperature, snow cover, and precipitation were not considered in the ordination. These factors are likely quite different at low and high elevations and are certainly influential to plant growth (Walker et al. 2016). For example, some mean summer temperatures in alpine sites can be close to freezing, effecting plant growth and species diversity (Figure 13).

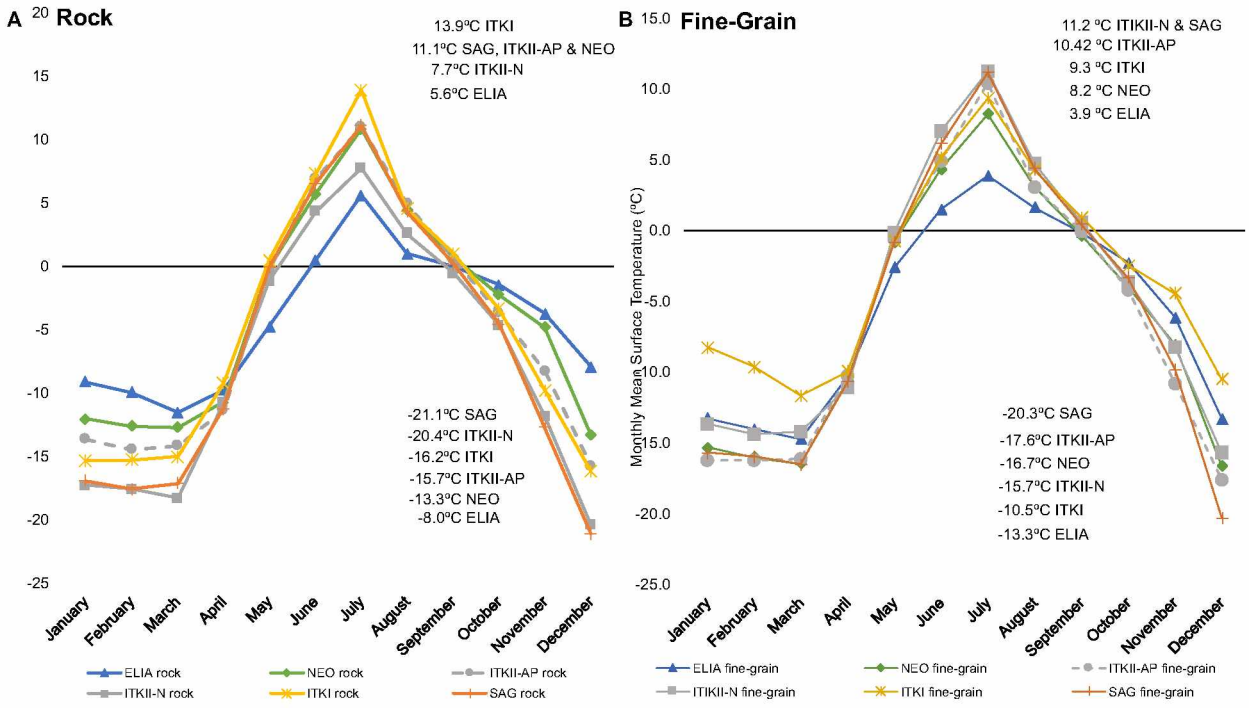

Figure 13. Monthly mean surface temperatures across all glacial deposits on fine-grain **(A)** and rock **(B)** relevés over one year (July 2017- July 2018). Data was collected via ibuttons placed just below the litter layer which logged temperature about six-time daily. Mean temperatures are based on daily temperature averages for each month. Temperatures written in text indicate the high and low monthly average temperature for each moraine over the year.

When directly comparing surface temperatures between alpine and foothill glacial deposits of similar ages, there is similarity on both substrates, especially on fine-grained sites over the course of one year (Figure 13; $p > 0.05$, $z = -0.3$, d.f. $= 11$), and over the last decade (Figure 4). However, decadal variation between high and low altitude sites separates alpine sites into bioclimatic subzone D and foothill sites into bioclimatic subzone E (Figure 4), affecting a variety of plant community characteristics (CAVM Mapping Team et al. 2003). Additionally, the importance of the influence of snow on plant growth and diversity as well as overall annual precipitation cannot be overlooked, and accurate measurements were not available for study sites included here. Mean annual precipitation accumulation recorded by the SNOTEL weather stations at Imnavait Creek and Atigun pass, show significantly different precipitation levels ($p <$

0.05, z =28.8, d.f. = 30) between high and low elevation sites, and very little change in accumulation since the 1980s (Figure 14).

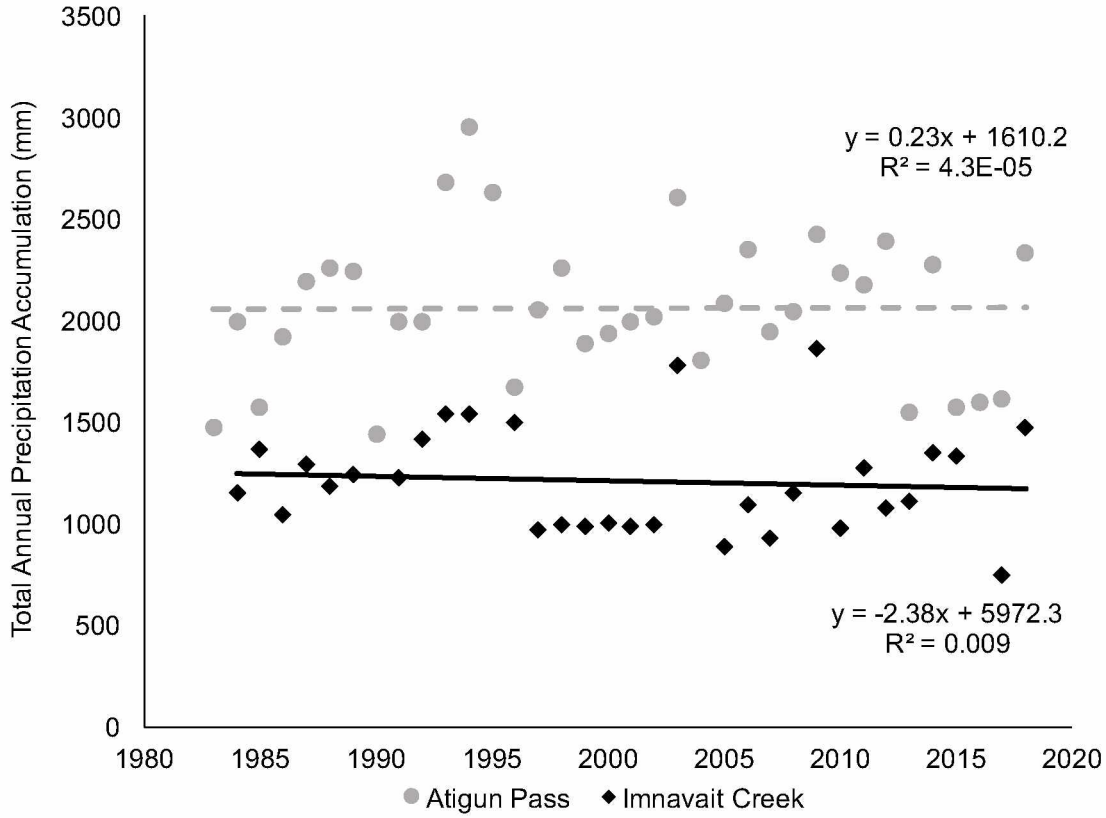

Figure 14. Mean annual precipitation accumulation (mm) for Atigun Pass (SNOTEL #957 **grey circles**) and Imnavait Creek (SNOTEL #968**, black diamonds**), from 1983-2018.

There is some overlap between factors which separate high and low elevation sites into bioclimatic subzones (e.g., mean July temperature, summer warmth index, & horizontal structure of plant cover; see CAVM Mapping Team et al. 2003), adding support to evidence suggesting that environmental factors alone do not account for variation between plant communities at low and high elevations in this system. Rather, the data show it is likely that time since exposure is the major driving influence along this chronosequence and elevational gradient. However, a more detailed analyses of environmental factors and climatic variation across the transect,

especially considering snow, would clarify which environmental factors are most influential in the separation of alpine and foothill communities.

The most striking differences between surface temperatures across the chronosequence and elevation gradient is seen in the alpine ELIA moraine's surface temperature variation on both rock and fine-grained substrates (Figure 13). This glacial deposit is located at the highest elevation site of the study, as is the NEO glacial deposit which differs much less overall in average monthly surface temperature than the rest of the glacial deposits regardless of altitude (Figure 13). All notable surface temperature differences across this chronosequence and elevational gradient occur almost exclusively on glacial deposits undergoing early stages of succession, particularly the ELIA glacial deposit, suggesting that a lack of vegetation cover and microclimate stability rather than altitude alone is likely contributing to surface temperature variations between glacial deposits. Another indicator of this is the nearly identical average monthly temperatures between the two ITKII glacial deposit surfaces in the alpine (ITKII-AP) and in the foothills (ITKII-N) (Figure 13, Table 3). In many months, (e.g., April, May, September, October) the average surface temperatures recorded on both substrates are very similar, and peak growing season (July) and peak winter (December) are nearly identical (Figure 13). The fact that mean monthly temperatures throughout the year are so similar at high elevation (ELIA, NEO & ITKII) and low elevation (ITKII-N, ITKI, & SAG) sites, suggests that in this system, temperature limitations at high altitudes might be minimized, especially for low-growing plants.

Further research

There are at least 70 alpine glacial cirques in the Central Brooks Range within a 1500 km^2 area of similar size and retreat status (Calkin and Ellis 1981) to the Grizzly Glacier. Forty of

these cirque glaciers were mapped during glacial surveys conducted in the late 1970s (Calkin and Ellis 1981), and thus moraine ages are known. In order to fully understand how arctic-alpine deglaciated cirques are undergoing primary succession post-deglaciation, a broader range of recently deposited moraines should be surveyed. Further surveys should include cirques underlain by different types of parent material representative of the area. Additionally, given the large separation of these time-steps it would be useful to monitor glacial deposits exposed during the end of the Little Ice Age, and their Neoglacial counterparts over the course of a few years to a decade to determine specific rates of primary succession. These efforts would clarify whether my findings are unique to the Grizzly Glacier, or if the patterns found here can be extended to other sites in the Central Brooks Range.

A more thorough and collaborative research effort focused on the factors controlling establishment and recruitment of pioneer species is essential to understanding and predicting how, and at what rate communities will form, and how disturbance might affect succession. This is especially important for cryptogams, which make up the majority of pioneer colonizers in this consequence and elevation gradient, and are generally underrepresented in successional studies. Throughout succession cryptogams are integral members of communities on all glacial deposits at all elevations here, and many are diagnostic species. However, very little is known about how cryptogams interact with vascular plants or sources of propagules for the establishment of pioneer taxa. Developing an understanding of the origins of these taxa, can allow for more accurate predictions of community development following disturbance and in response to environmental change, and form a more complete understanding of factors controlling community assembly and recruitment. Additionally, a variety of environmental variables that are likely influential to vegetation community formation were outside the scope of this study. Thus,

a closer investigation of environmental differences on high and low altitude glacial deposit ridges would help clarify which factors are most influential to community formation.

Conclusions

Succession in the high alpine of the Central Brooks Range begins almost immediately following deglaciation, with small communities forming within 40 years. However, this process is slow and directional, taking thousands of years for mature communities to assemble, interactions to take place, and changes to occur. It is highly advantageous throughout all stages of succession, and at all elevations to be symbiotic. This is advantage is shown here by macrolichens being the most speciose growth form throughout, dominant on many sites, and the most common to persist in communities at later stages of succession. Although there is an obvious influence of altitude on plant communities in this sequence, it is likely buffered by similarities between conditions on glacial deposits in the alpine and in the foothills (e.g., wind exposure, soil texture, pH, stability, and surface temperature). Thus, time since exposure is an especially powerful driving factor of variation between plant communities in this system.

New alpine habitats resulting from this process will provide valuable alpine resources and refugia to flora and fauna, at a crucial time of rapid and pronounced arctic change, which could prove valuable in maintaining species important to ecosystem function in future years. However, given the incredibly slow nature of succession in this environment, developing communities should be considered, from a conservation perspective, as sensitive ancient communities worthy of protection. Thus, more extensive documentation and research on the successional process in cirque glacial forelands should be a priority for Arctic ecologists, as the opportunity for

witnessing pioneer succession unfold in these areas is available now, and only for a limited window of time.

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Appendices

Appendix A: Plot Photos

Grizzly Glacier: ELIA glacial deposit fine-grain (N=3)

ELIA-113

ELIA-114

ELIA-115

Grizzly Glacier: NEO glacial deposit fine-grain (N=3)

NEO-108

NEO-110

NEO-112

Atigun pass: ITKII-AP fine-grain (N=4)

ITKII-AP-1

ITKII-AP-5

ITKII-AP-123

ITKII-AP-124

Foothills: ITKII-N fine-grain (N=5)

ITKII-N-103

ITKII-N-104

ITKII-N-137

ITKII-N-135

ITKII-N-137

Foothills: ITKI fine-grain (N=3)

ITKI-127 ITKI-129 ITKI-131

Foothills: SAG fine-grain (N=3)



SAG-105 SAG-107 SAG-121

Grizzly Glacier: ELIA rock (N=3)



ELIA-116 ELIA-117 ELIA-118

Grizzly Glacier: NEO rock (N=3)



NEO-109 NEO-111 NEO-118

Atigun Pass: ITKII-AP rock (N=4)

ITKII-AP-2

ITKII-AP-3

ITKII-AP-4

ITKII-AP-125

Foothills: ITKII-N rock (N=5)

ITKII-N-101

ITKII-N-102

ITKII-N-132

ITKII-N-134

ITKII-N-136

Foothills: ITKI rock (N=3)

ITKI-126

ITKI-128

ITKI-130

Foothills: SAG rock (N=3)

SAG-106

SAG-120

SAG-122

Appendix B: Synoptic Table

Full synoptic table for statistical clusters of plant communities within plots along the alpine-foothills elevational gradient, and glacial chronosequence. Clusters are defined by substrate type (**fine-grain or rock**), elevation (**alpine or foothills**), and glacial deposit (ELIA, NEO, ITKII, ITKI, SAG). Codes in the second column represent growth forms as follows: (**bl**) bryophyte liverwort, (**bm**) bryophyte moss, (**cl**) crustose lichen, (**ds**) dwarf shrub, (**ef**) erect forb, (**fol**) foliose lichen, (**frl**) fruticose lichen, (**gra**) grass, (**ls**) low shrub, (**mcf**) mat or cushion forb, (**rus**) rush, (**sed**) sedge, (**svp**) seedless vascular plant. Values in columns three through nine indicate frequency of the given plant species within each cluster. Diagnostic species for each cluster were calculated using fidelity values indicated by the phi coefficient (Chytrý et al. 2002). Diagnostic taxa are ordered by descending fidelity values. Frequency values of taxa with the highest fidelity (phi > 0.8) for a cluster are highlighted in dark grey, those with high fidelity (phi ≥ 0.5) are highlighted in medium-grey, and those with somewhat high fidelity (phi ≥ 0.4) are highlighted in light grey. Frequency values marked with an asterisk indicate statistically significant (p <0.05) fidelity to a cluster according to a Monte Carlo randomization test. Average cover values (%) for each diagnostic taxon in a given cluster are indicated as superscript.

Cluster number		**1**	**2**	**3**	**4**	**5**	**6**	**7**
Substrate		**Fine-grain**	**Rock**	**Fine-grain**	**Fine-grain**	**Rock**	**Rock**	**Fine-grain & Rock**
Elevation		**Alpine**	**Alpine**	**Alpine**	**Foothills**	**Alpine**	**Foothills**	**Foothills**
Glacial deposit		**ELIA & NEO**	**ELIA & NEO**	**NEO & ITKII**	**ITKII & SAG**	**ITKII, (SAG)**	**ITKII, ITKI & SAG**	**ITKII-N**
Number of relevés		**4**	**6**	**6**	**6**	**5**	**8**	**7**
Diagnostic taxa for Cluster 1: *C. latifolium, P. didactyla* comm.								
Chamerion latifolium	**ef**	**100*^{1}**	-	17	-	-	-	-
Peltigera didactyla	**fol**	**100*$^{+}$**	-	33	-	-	13	29
Salix arctica	**ds**	**75*$^{+}$**	-	17	-	-	-	14
Peltigera venosa	**fol**	**50*$^{+}$**	-	17	-	-	-	-
Saxifraga punctata	**ef**	**25^{1}**	-	-	-	-	-	-
Solorina saccata	**fol**	**25^{R}**	-	-	-	-	-	-
Trisetum spicatum	**gra**	**25^{+}**	-	-	-	-	-	-
Diagnostic taxa for cluster 2: *Lecanora polytropa, Candellariella vitellina* comm.								
Lecanora polytropa	**cl**	-	**100*$^{+}$**	-	-	-	-	29
Candellariella vitellina	**cl**	-	**100*$^{+}$**	-	-	-	-	43
Umbilicaria cylindrica	**fol**	-	**100*^{3}**	-	-	60	-	-
Campylium stellatum	**bm**	50	**67^{+}**	67	-	-	-	-
Diagnostic taxa for cluster 3: *Salix rotundifolia* & *Racomitrium lanuginosum* comm.								
Salix rotundifolia	**ds**	-	-	**67*^{5}**	17	-	-	-
Dactylina ramulosa	**frl**	-	-	**83*$^{+}$**	33	20	13	-

Saxifraga cernua	**ef**	25	17	**67*^{1}**	-	-	-	-
Draba macrocarpa	**ef**	-	-	**50*$^{+}$**	-	-	-	14
Luzula confusa	**rus**	-	-	**33^{+}**	-	-	-	-
Saxifraga razshivinii	**ef**	-	-	**33^{1}**	-	-	-	-
Poa paucispicula	**gra**	25	-	**50^{+}**	-	-	13	-
Potentilla uniflora	**ef**	-	-	**50^{1}**	-	-	13	14
Stereocaulon alpinum	**frl**	-	17	**50^{1}**	-	20	-	-
Racomitrium lanuginosum	**bm**	-	17	**100*^{5}**	33	100	50	14
Aulacomnium turgidum	**bm**	-	-	**50^{+}**	17	-	-	29
Cardamine bellidifolia	**ef**	-	17	**33^{+}**	-	-	-	-
Papavar lapponicum	**ef**	-	17	**33^{R}**	-	-	-	-
Solorina crocea	**fol**	-	-	**33^{+}**	-	20	-	-
Psoroma hypnorum	**cl**	50	17	**83^{+}**	67	40	-	14
Diagnostic taxa for cluster 4: *Betula nana* and *Masonhalea richardsonii comm.*								
Cassiope tetragona	**ls**	-	-	-	**67*$^{+}$**	-	13	-
Masonhalea richardsonii	**fol**	-	-	-	**100*$^{+}$**	20	25	29
Vaccinium vitis-idaea	**ls**	-	-	-	**83*^{8}**	20	25	-
Cladonia sulphurina	**frl**	-	-	17	**100*$^{+}$**	20	38	14
Betula nana	**ds**	-	-	-	**67*^{9}**	-	25	-
Peltigera canina	**fol**	-	-	17	**67*$^{+}$**	-	13	-
Cladonia bellidiflora	**frl**	-	-	-	**50*^{R}**	-	13	-
Diapensia lapponica	**mcf**	-	17	-	**50*$^{+}$**	-	-	-
Polygonum bistorta	**ef**	-	-	-	**50*$^{+}$**	-	13	-
Sticta arctica	**fol**	-	-	-	**50*$^{+}$**	-	13	-
Poa alpina	**gra**	-	-	17	**83*^{1}**	20	13	43
Vaccinium uliginosum	**ls**	-	-	-	**67*^{1}**	20	13	29
Cladonia acuminata	**frl**	-	-	-	50^{+}	-	25	-
Flavocetraria cucullata	**fol**	25	-	33	**100*$^{+}$**	20	38	71
Artemisia arctica	**ef**	-	-	-	33^{+}	-	-	14
Petisites frigidus	**ef**	-	-	17	40^{1}	-	-	-
Salix phlebophylla	**ds**	50	-	33	83^{1}	-	13	71
Diagnostic taxa for cluster 5: *Porpidia flavocaerulescens, Cladonia squamosa* comm.								
Cetraria nigricans	**fol**	-	-	-	-	**60*$^{+}$**	-	-
Schaereria endocyanea	**cl**	-	-	-	-	**40*^{R}**	-	-
Schistidium apocarpum	**bm**	-	-	-	-	**40*$^{+}$**	-	-
Umbilicaria torrefecta	**fol**	-	-	-	-	**40*$^{+}$**	-	-
Porpidia flavocaerulescens	**cl**	-	67	-	-	**100*$^{+}$**	50	-
Cladonia squamosa	**frl**	-	-	-	17	**80*$^{+}$**	63	-

Tortella tortuosa	**bm**	25	33	-	-	**60*$^{+}$**	-	-
Cladonia subfurcata	**frl**	-	-	-	-	40^{+}	13	-
Cetraria ericetorum	**fol**	-	-	67	50	100^{+}	75	-
Cladonia pyxidata	**frl**	50	17	83	33	100^{+}	-	43
Amygdalaria panaeola	**cl**	-	-	-	-	20^{1}	-	-
Equisetum arvense	**svp**	-	-	-	-	20^{+}	-	-
Ochrolechia inaequatula	**cl**	-	-	-	-	20^{R}	-	-
Stereocaulon arenarium	**frl**	-	-	-	-	20^{R}	-	-
Stereocaulon botryosum	**frl**	-	-	-	-	20^{+}	-	-
Umbilicaria arctica	**fol**	-	-	-	-	20^{1}	-	-
Pseudephebe pubescens	**cl**	-	-	-	-	40^{1}	13	14
Umbilicaria proboscidea	**fol**	-	17	-	-	60^{1}	50	14
Cetrariella delisei	**fol**	-	-	33	33	40^{1}	-	-
Diagnostic taxa for cluster 6: *Arctoparmelia centrifuga* & *Ophioparma lapponicum* comm.								
Ophioparma lapponica	**cl**	-	-	-	-	20	**100*$^{+}$**	29
Arctoparmelia centrifuga	**fol**	-	-	-	-	60	**100*^{4}**	29
Asahinea scholanderi	**fol**	-	-	-	-	-	**50*$^{+}$**	14
Rhizocarpon cinereovirens	**cl**	-	67	-	-	20	**75*^{3}**	-
Parmelia omphalodes	**fol**	-	17	17	-	100	**100*^{2}**	57
Tetralophozia setiformis	**bl**	-	-	33	-	80	**88*^{1}**	29
Carex bigelowii	**sed**	-	-	-	17	-	**50^{+}**	14
Lecidea lactea	**cl**	-	-	-	-	-	25^{+}	-
Rhizocarpon geographicum	**cl**	-	83	-	-	100	**100*^{2}**	29
Umbilicaria krascheninnikovii	**fol**	-	-	-	-	20	38^{1}	-
Asahinea crysantha	**fol**	-	-	-	20	33	**88*$^{+}$**	86
Cladina rangiferina	**frl**	-	-	33	100	60	**100*^{1}**	43
Umbilicaria hyperborea	**fol**	-	100	17	-	100	**100*^{2}**	29
Allocetraria madreporiformis	**frl**	-	-	17	-	20	50^{+}	14
Diagnostic taxa for cluster 7: *Mixed community transitional cluster.*								
Dryas integrifolia	**ef**	25	-	-	17	-	-	**100*^{23}**
Hypogymnia austerodes	**fol**	-	-	-	-	-	38	**100*$^{+}$**
Antennaria friesiana	**ef**	-	-	-	-	-	-	**57*^{1}**
Oxytropis jordalii	**ef**	-	-	-	-	-	-	**57*^{1}**
Pedicularis lanata	**ef**	-	-	-	-	-	-	**57*$^{+}$**
Tomenthypnum nitens	**bm**	-	-	17	-	-	13	**71*^{3}**
Ochrolechia upsaliensis	**cl**	-	-	-	-	-	-	**43*$^{+}$**
Bistorta vivipara	**ef**	-	-	-	-	33	-	**57*$^{+}$**

Lobaria linita	**fol**	-	-	17	17	-	-	**57*$^{+}$**
Lecanora epibryon	**cl**	-	-	-	-	-	-	29^{1}
Pedicularis capitata	**ef**	-	-	-	-	-	-	29^{+}
Ptilidium ciliare	**bl**	-	-	-	-	-	-	29^{+}
Rhytidium rugosum	**bm**	-	-	-	-	-	-	29^{1}
Kobresia myosuroides	**sed**	25	-	-	-	-	-	**43*^{1}**
Cladonia pocillum	**frl**	25	-	-	17	-	38	**71*$^{+}$**
Carex microchaeta	**sed**	-	-	67	50	-	13	**86*$^{+}$**
Peltigera leucophlebia	**fol**	-	-	33	67	20	13	**86*$^{+}$**
Bryocaulon divergens	**frl**	-	-	17	-	-	25	**57*$^{+}$**
Non-diagnostic taxa occurring in multiple clusters								
Polytrichum juniperinum	**bm**	100	50	100	33	60	75	86
Stereocaulon paschale	**frl**	50	33	67	50	80	38	14
Cladonia gracilis	**frl**	25	17	67	100	100	100	43
Thamnolia vermicularis	**frl**	25	-	67	83	80	88	100
Dactylina arctica	**frl**	-	17	83	100	60	75	71
Pseudephebe minuscula	**frl**	-	50	17	-	20	13	29
Sphaerophorus globosus	**frl**	-	33	17	17	-	13	14
Dicranoweisia crispula	**bm**	-	-	83	100	40	100	43
Cladonia uncialis	**frl**	-	-	67	100	100	25	100
Cetraria kamczatica	**fol**	-	-	67	83	60	100	100
Cladonia stygia	**frl**	-	-	50	83	60	75	14
Pertusaria dactylina	**cl**	-	-	50	83	60	100	71
Flavocetraria nivalis	**fol**	-	-	50	83	40	100	86
Alectoria ochroleuca	**frl**	-	-	33	83	40	50	57
Cladonia arbuscula	**frl**	-	-	33	67	20	13	57
Gowardia nigricans	**frl**	-	-	33	100	40	100	100
Ochrolechia frigida	**cl**	-	-	17	17	20	13	43
Cladonia chlorophaea	**frl**	-	17	-	17	20	13	-
Cladonia multiformis	**frl**	-	-	17	17	20	38	-
Hylocomium splendens	**bm**	-	-	50	17	-	25	14
Allantoparmelia alpicola	**cl**	-	-	33	-	25	25	29
Ceratodon purpureus	**bm**	50	33	33	-	-	-	-
Bryum arcticum	**bm**	25	17	33	-	-	-	-
Stereocaulon rivulorum	**frl**	25	33	-	-	20	-	-
Salix reticulata	**ds**	25	-	17	-	-	-	29
Dicranum groenlandicum	**bm**	-	-	33	17	-	-	14
Stellaria longipes	**ef**	-	-	50	-	-	25	29
Dicranum flagellare	**bm**	-	-	17	17	-	-	14
Cladonia coccifera	**frl**	-	-	-	17	20	13	-

Cladonia deformis	**frl**	-	-	-	33	20	13	-
Rhododendron tomentosum	**ls**	-	-	-	50	-	25	43
Dicranum fragilifolium	**bm**	-	-	-	17	-	38	29
Polytrichum hyperboreum	**bm**	25	17	-	-	-	-	-
Poa pseudoabbreviata	**gra**	-	-	33	-	-	-	29
Saxifraga bronchialis	**mcf**	-	-	33	-	-	-	29
Oxyria digyna	**ef**	-	-	17	-	-	-	14
Calamagrostis canadensis	**gra**	-	-	-	33	-	38	-
Arnica frigida	**ef**	-	-	-	17	-	13	-
Nephroma arcticum	**fol**	-	-	-	17	-	13	-
Polytrichum strictum	**bm**	-	-	-	17	-	13	-
Dicranum scoparium	**bm**	-	-	-	17	-	-	29
Arctous alpine	**ls**	-	-	-	17	-	-	14
Nephroma expallidum	**fol**	-	-	-	17	-	-	14
Melanelia stygia	**fol**	-	-	-	-	40	-	43
Festuca baffinensis	**gra**	-	-	-	-	20	-	14
Parmelia sulcata	**fol**	-	-	-	-	20	-	14
Protopannaria badia	**fol**	-	-	-	-	20	-	14
Phlox siberica	**ef**	-	-	-	-	-	13	29
Selaginella sibirica	**svp**	-	-	-	-	-	13	29
Dicranum elongatum	**bm**	-	-	-	-	-	13	29
Non-diagnostic Singly Occurring Species								
Gimmia longirostris	**bm**	-	17	-	-	-	-	-
Kiaeria starkei	**bm**	-	17	-	-	-	-	-
Syntrichia norvegica	**bm**	-	17	-	-	-	-	-
Tortula mucronifolia	**bm**	-	17	-	-	-	-	-
Xanthoria elegans	**cl**	-	17	-	-	-	-	-
Cerastium beeringianum	**ef**	-	-	17	-	-	-	-
Cetraria laevigata	**fol**	-	-	17	-	-	-	-
Cladonia amauocraea	**frl**	-	-	17	-	-	-	-
Montia bostockii	**ef**	-	-	17	-	-	-	-
Luzula arcuata	**rus**	-	-	17	-	-	-	-
Pertusaria bryontha	**cl**	-	-	17	-	-	-	-
Poa arctica	**gra**	-	-	17	-	-	-	-
Protopannaria pezizoides	**cl**	-	-	17	-	-	-	-
Saxifraga oppositifolia	**mcf**	-	-	17	-	-	-	-
Carex atrofusca	**sed**	-	-	-	17	-	-	-
Cladonia macrophylla	**frl**	-	-	-	17	-	-	-

Cladonia stellaris	**frl**	-	-	-	17	-	-	-
Hierochloe alpine	**gra**	-	-	-	17	-	-	-
Pyrola grandiflora	**ef**	-	-	-	17	-	-	-
Rubus chamaemorus	**ls**	-	-	-	17	-	-	-
Brodoa oroarctica	**cl**	-	-	-	-	-	13	-
Calvitimela armeniaca	**cl**	-	-	-	-	-	13	-
Dryas octopetala	**ef**	-	-	-	-	-	13	-
Pohlia cruda	**bm**	-	-	-	-	-	13	-
Eurybia siberica	**ef**	-	-	-	-	-	-	14
Bupleurum americanum	**ef**	-	-	-	-	-	-	14
Melanelia hepatizon	**fol**	-	-	-	-	-	-	14
Cetraria muricata	**fol**	-	-	-	-	-	-	14
Encalypta rhaptocarpa	**bm**	-	-	-	-	-	-	14
Encalypta vittiana	**bm**	-	-	-	-	-	-	14
Oxytropis maydelliana	**ef**	-	-	-	-	-	-	14
Peltigera rufescens	**fol**	-	-	-	-	-	-	14
Pertusaria panyrga	**cl**	-	-	-	-	-	-	14
Pertusaria subobducens	**cl**	-	-	-	-	-	-	14
Pleurozium schreberi	**bm**	-	-	-	-	-	-	14
Pohlia nutans	**bm**	-	-	-	-	-	-	14
Polytrichum piliferum	**bm**	-	-	-	-	-	-	14
Rhododendron lapponicum	**ls**	-	-	-	-	-	-	14
Ropalospora lugubris	**cl**	-	-	-	-	-	-	14
Tofieldia coccinea	**ef**	-	-	-	-	-	-	14
Vupicida tilesii	**fol**	-	-	-	-	-	-	14

Appendix C: Species List

Lichens (N =98)

Alectoria ochroleuca, (Hoffm.) A. Massal., Parmeliaceae
Allantoparmelia alpicola, (Th. Fr.) Essl., Parmeliaceae
Allocetraria madreporiformis, (Ach.) Kärnefelt & Thell., Parmeliaceae
Amygdalaria panaeola, (Ach.), Hertel & Brodo., Lecideaceae
Arctoparmelia centrifuga, (L.) Hale., Parmeliaceae
Asahinea crysantha, (Tuck.) Culb. & C. Culb., Parmeliaceae
Asahinea scholanderi, (Llano) Culb. & C. Culb., Parmeliaceae
Brodoa oroarctica, (Krog) Goward, Parmeliaceae
Bryocaulon divergens, (Ach.) Kärnefelt., Parmeliaceae
Calvitimela armeniaca, (DC.) Haffelner, Lecanoraceae
Candellariella vitellina, (Hoffm.) Müll. Arg., Candelariaceae
Cetraria ericetorum, Opiz., Parmeliaceae
Cetraria kamczatica, Savicz., Parmeliaceae
Cetraria laevigata, Rass., Parmeliaceae
Cetraria muricata, (Ach.), Eckfeldt. Parmeliaceae
Cetraria nigricans, (Nyl.), Parmeliaceae
Cetrariella delisei, (Bor ex Schaer.) Kärnefelt & Thell, Parmeliaceae
Cladina rangiferina, (L.) Nyl., Cladoniaceae
Cladina stygia, (Fr.) Ruoss, Cladoniaceae
Cladonia acuminata, (Ach.) Norrlin., Cladoniaceae
Cladonia amauocraea, (Flörke) Schaer., Cladoniaceae
Cladonia arbuscula, (Wallr.) Rabenh., Cladoniaceae
Cladonia bellidiflora, (Ach.) Schaer., Cladoniaceae
Cladonia chlorophaea, (Flörke ex Sommerf.) Sprengel, Cladoniaceae
Cladonia cocciferea, (L.) Willd., Cladoniaceae
Cladonia deformis, (L.) Hoffm., Cladoniaceae
Cladonia ecmocyna, Leighton, Cladoniaceae
Cladonia gracilis, (L.) Willd., Cladoniaceae
Cladonia macrophylla, (Schaer.) Stenh., Cladoniaceae
Cladonia multiformis, G. Merr., Cladoniaceae
Cladonia pocillum, (Ach.) O.J. Rich., Cladoniaceae
Cladonia pyxidata, (L.) Hoffm., Cladoniaceae
Cladonia stellaris, (Opiz) Pouzar & Vězda, Cladoniaceae
Cladonia subfurcata, (Nyl.) Arnold, Cladoniaceae
Cladonia sulphurina, (Michaux) Fr., Cladoniaceae
Cladonia uncialis, (L.) F. H. Wigg, Cladoniaceae
Dactylina arctica, (Richardson) Nyl., Parmeliaceae
Dactylina ramulosa, (Hook) Tuck, Parmeliaceae
Flavocetraria cucullata, (Bellardi) Kärnefelt & Thell, Parmeliaceae
Flavocetraria nivalis, (L.) Kärnefelt & Thell, Parmeliaceae
Gowardia nigricans, (Ach.) P. Halonen L. Myllys S. Velmala & H. Hyvarinen, Parmeliaceae
Hypogymnia austerodes, (Nyl.) Räsänen, Parmeliaceae
Lecanora epibryon, (Ach.) Ach., Lecanoraceae

Lecanora polytropa, (Hoffm.) Rabenh., Lecanoraceae
Lecanora sp., Lecanoraceae
Lecidea sp., Lecideaceae
Lecidea lactea, Flörke ex Schaer., Lecideaceae
Lobaria linita, (Ach.) Rabenh., Lobariaceae
Masonhalea richardsonii, (Hook.) Kärnefelt, Parmeliaceae
Melanelia hepatizon, (Ach.) Thell., Parmeliaceae
Melanelia stygia, (L.) Ess., Parmeliaceae
Nephroma arcticum, (L.) Torss., Nephromataceae
Nephroma expallidum, (Nyl.) Nyl., Nephromataceae
Ochrolechia frigida, (Sw.) Lynge, Ochrolechiaceae
Ochrolechia inaequatula, (Nyl.) Zahlbr., Ochrolechiaceae
Ochrolechia upsaliensis, (L.) A. Massal., Ochrolechiaceae
Ophioparma lapponica, (Räsänen) Hafellner & R.W. Rogers, Ophioparmaceae
Parmelia omphalodes, (L.) Ach., Parmeliaceae
Parmelia sulcata, Taylor, Parmeliaceae
Peltigera canina, (L.) Wild, Peltigeraceae
Peltigera didactyla, (With.) J.R. Laundon, Peltigeraceae
Peltigera leucophlebia, (Nyl.) Gyelnick, Peltigeraceae
Peltigera venosa, (L.) Hoffm., Peltigeraceae
Peltigera rufescens, (Weiss) Humb., Peltigeraceae
Pertusaria bryontha, (Ach.) Nyl., Pertusariaceae
Pertusaria dactylina, (Ach.) Nyl., Pertusariaceae
Pertusaria panyrga, (Ach.) A. Massal, Pertusariaceae
Pertusaria subobducens, Nyl., Pertusariaceae
Physcia sp., Physciaceae
Porpidia flavocaerulescens, (Hornem.) Hertel & A. J. Schwab, Lecideaceae
Protopannaria badia, (Hoffm.) Haffellner, Lecanoraceae
Protopannaria pezizoides, (Weber ex F.H. Wigg.) P.M. Jørg. & S. Ekman, Pannariaceae
Pseudephebe minuscula, (Nyl. Ex Arnold) Brodo & D. Hawksw., Parmeliaceae
Pseudephebe pubescens, (L.) Choisy, Parmeliaceae
Psoroma hypnorum, (Vahl) Gray., Pannariaceae
Rhizocarpon cinereovirens, (Müll. Arg.) Vain., Rhizocarpaceae
Rhizocarpon disporum, (Naeg. Ex Hepp) Müll. Arg, Rhizocarpaceae
Rhizocarpon geographicum, (L.) DC., Rhizocarpaceae
Ropalospora lugubris, (Sommerf.) Poelt., Ropalosporaceae
Schaereria endocyanea, (Stirt.) Hertel & Gotth. Schneid., Schaereriaceae
Solorina crocea, (L.) Ach., Peltigeraceae
Solorina saccata, (L.) Ach., Peltigeraceae
Sphaerophorus globosus, (Hudson) Vain., Spaerophoraceae
Stereocaulon alpinum, Laurer ex Funck, Stereocaulaceae
Stereocaulon arenarium, (Savicz) Lamb, Stereocaulaceae
Stereocaulon botryosum, (Ach.), Stereocaulaceae
Stereocaulon paschale, (L.) Hoffm., Stereocaulaceae
Stereocaulon rivulorum, H. Magn., Stereocaulaceae
Sticta arctica, Degel., Lobariaceae

Thamnolia vermicularis, (Sw.) Ach. Ex Schaer., Icmadophilaceae
Umbilicaria arctica, (Ach.) Nyl., Umbilicariaceae
Umbilicaria cylindrica, (L.) Baumg., Umbilicariaceae
Umbilicaria hyperborea, (Ach.) Hoffm., Umbilicariaceae
Umbilicaria krascheninnikovii, (Savicz) Zahlbr., Umbilicariaceae
Umbilicaria proboscidea, (L.) Schrader, Umbilicariaceae
Umbilicaria torrefecta, (Lightf.) Schrader, Umbilicariaceae
Vupicida tilesii, (Ach.) J.-E. Mattsson & M.J. Lai, Parmeliaceae
Xanthoria elegans, (Link) Th. Fr., Teloschistaceae

Mosses (N=37)
Aulacomnium turgidum, (Wahlenberg) Schwagrichen, Aulacomniaceae
Brachythecium sp., Brachythecieaceae
Bryum arcticum, (R. Br.) Bruch, Schimp. & W. Guembel., Bryaceae
Bryum sp., Bryaceae
Campylium stellatum, (Hedwig) C.E.O. Jensen Meddel. Grøland., Amblystegiaceae
Ceratodon purpureus, (Hedw.) Brid., Ditrichaceae
Dicranoweisia crispula, (Hedw.) Milde, Seligeriaceae
Dicranum sp., Dicranaceae
Dicranum elongatum, Schleich ex. Schwägr, Dicranaceae
Dicranum flagellare, Hedw., Dicranaceae
Dicranum fragilifolium, Lindb., Dicranaceae
Dicranum groenlandicum, Brid., Dicranaceae
Dicranum scoparium, Hedw., Dicranaceae
Drepnocladus sp., Amblystegiaceae
Encalypta rhaptocarpa, Schwägr, Encalyptaceae
Encalypta vittiana, D.G. Horton, Encalyptaceae
Gimmia longirostris, Hook., Grimmiaceae
Hylocomium splendens, (Hedwig) Schimper, Hylocomiaceae
Kiaeria starkei, (Weber & D. Mohr) I. Hagen, Dicranaceae
Mnium sp., Mniaceae
Niphotrichum sp., Grimmiaceae
Pleurozium schreberi, (Brid.) Mitt., Hylocomiaceae
Pohlia cruda, (Hedwig) Lindberg Musc. Scand., Mielichhoferiaceae
Pohlia nutans, (Hedwig) Lindberg Musc. Scand., Mielichhoferiaceae
Pohlia sp., Mielichhoferiaceae
Polytrichum hyperboreum, R. Brown Chlor. Melvill., Polytrichaceae
Polytrichum juniperinum, (Hedw.), Polytrichaceae
Polytrichum piliferum, Hedwig, Polytrichaceae
Polytrichum strictum, Bridel J. Bot. (Schrader)., Polytrichaceae
Polytrichum sp., Polytrichaceae
Racomitrium lanuginosum, (Hedwig) Bridel Muscol., Grimmiaceae
Rhytidium rugosum, (Hedw.) Kindb., Rhytidiaceae
Schistidium apocarpum, (Hedw.) Bruch & Schimp., Grimmiaceae
Syntrichia norvegica, F. Weber, Arch., Pottiaceae
Tomenthypnum nitens, (Hedw.) Loeske, Brachythecieaceae

Tortula mucronifolia, Schwägr., Pottiaceae
Tortella tortuosa, (Hedw.) Limpr., Pottiaceae

Liverworts (N =3)
Ptilidium ciliare, (L.) Hampe, Ptilidiaceae
Riccardia sp., A. Gray., Aneuraceae
Tetralophozia setiformis, (Ehrh.) Schljakov, Jungermanniaceae

Seedless Vascular Plants (N =2)
Equisetum arvense, (L.), Equisetaceae
Selaginella sibirica, (Milde) Hieron., Selaginellaceae

Grasses (N =7)
Calamagrostis canadensis, (Michx.) P. Beauv., Subsp. canadensis., Poaceae
Hierochloe alpine, (Sw.) Roem. & Schult., Poaceae
Kobresia myosuroides, (Vill.) Fiori, Cyperaceae
Poa arctica, R. Br., subsp. arctica, Poaceae
Poa paucispicula, Scribn. & Merr., Poaceae
Poa pseudoabbreviata, Roshev., Poaceae
Trisetum spicatum, (L.) K. Richt, Poaceae

Rushes (N =2)
Luzula arcuata, (Wahlenb.), Juncaceae
Luzula confusa, Lindeb., Juncaceae

Sedges (N =3)
Carex atrofusca, Schkuhr., Cyperaceae
Carex bigelowii, Torr., Cyperaceae
Carex microchaeta, Holm., Cyperaceae

Forbs (N =35)
Antennaria friesiana, (Trautv.) Ekman., Asteraceae
Arnica frigida, C.A. Mey. Ex Iljin., Asteraceae
Bistorta vivipara, (L.) Delarbre., Polygonaceae
Bupleurum americanum, J.M. Coult. & Rose, Apiaceae
Chamerion latifolium, (L.), Onagraceae
Cardamine bellidifolia, (L.), Brassicaceae
Chamerion latifolium, (L.) Holub, Onagraceae
Cerastium beeringianum, Cham. & Schltdl., Caryophyllaceae
Diapensia lapponica, (L.), Diapensiaceae
Draba macrocarpa, Boiss. & Heldr., Brassicaceae
Dryas integrifolia, Vahl, Rosaceae
Dryas octopetala, L., Rosaceae
Eurybia siberica, (L.) G.L. Nesom., Asteraceae
Montia bostockii, (A.E. Porsild) S.L. Welsh, Portulaceae
Oxyria digyna, (L.) Hill, Polygonaceae

Oxytropis jordalii, A.E. Porsild, Fabaceae
Oxytropis maydelliana, Trautv., Fabaceae
Papavar lapponicum, (Tolm.) Nordh., Subp. occidentale, (C.E. Lundstr.) Knaben, Papaveraceae
Pedicularis capitata, Adams, Orobanchaceae
Pedicularis lanata, Cham. Schlect., Orobanchaceae
Petisites frigidus, (L.) Fr., subsp. frigidus
Phlox siberica, (L.), Polemoniaceae
Polygonum bistorta, (L.), Polygonaceae
Potentilla sp., Rosaceae
Potentilla uniflora, Ledeb., Rosaceae
Pyrola grandiflora, Radius, Ericaceae
Saxifraga bronchialis, (L.), Saxifragaceae
Saxifraga cernua, (L.), Saxifragaceae
Saxifraga oppositifolia, (L.), Saxifragaceae
Saxifraga punctata, (L.), Saxifragaceae
Saxifraga razshivinii, Zhmylev., Saxifragaceae
Saxifraga sp., Saxifragaceae
Tephroseris atropurpurea, (Ledeb.) Holub, ssp. atropurpurea, Asteraceae
Stellaria longipes, Goldie, ssp. longipes, Caryophyllaceae
Tofieldia coccinea, Richardson, Tofieldiaceae

Shrubs (N =13)
Arctous alpine, (L.) Nied., Ericaceae
Artemisia arctica, Less., Asteraceae
Betula nana, (L.), subsp. nana, Betulaceae
Cassiope tetragona, (L.) D. Don, Ericaceae
Rhododendron tomentosum, (Stokes) Harmaja, subsp. decumbens, (Alton) Elven & D.F. Murray, Ericaceae
Rhododendron lapponicum, (L.) Whalenb., Ericaceae
Rubus chamaemorus, (L.), Rosaceae
Salix arctica, Pall., Salicaceae
Salix phlebophylla, Andersson, Salicaceae
Salix reticulata, (L.), Salicaceae
Salix rotundifolia, Trautv., var. rotundifolia, Salicaceae
Vaccinium uliginosum, (L.), Ericaceae
Vaccinium vitis-idaea, (L.), Ericaceae

Total species richness =200
Lichens =49%
Mosses =18.5%
Forbs =17.5%
Shrubs =6.5%
Grasses =3.5%
Sedges =1.5%
Liverworts =1.5 %
Seedless Vascular Plants =1%

Rushes =1%

Appendix D: Percent Cover

Table A1. Percent cover and mean canopy heights of plant growth forms measured on each glacial surface **rock substrates**. Values in bold are the highest cover value or canopy height for a given growth form. Canopy height was measured in centimeters and cover percentages were estimated.

Rock Average Percent Live Cover												
	ELIA	St. Dev.	**NEO**	St. Dev.	**ITKII-AP**	St. Dev	**ITKII-N**	St. Dev	**ITKI**	St. Dev	**SAG**	St. Dev
Evergreen shrubs	0	± 0	0	± 0	0	± 0	0.5	± 0.4	**7**	± 12	1	± 2
Deciduous shrubs	0	± 0	0	± 0	3	± 5	0.5	± 0	**7**	± 12	0.5	± 0.3
Erect forbs	0	± 0	0.5	±	0.5	±	0.5	± 0	0.5	± 0	0.5	± 0
Mat and cushion forbs	0	± 0	0	± 0	0.5	± 0.1	**23**	± 31	0	± 0	0	± 0
Total graminoids	0	± 0	0.5	± 0.3	**3**	± 5	0.5	± 0.5	1	± 1	0.5	± 0.3
Seedless vascular plants	0	± 0	0	± 0	0	± 0	0.5	± 0.4	0	± 0	0.5	±
Foliose lichen	20	± 17.3	20	± 19.8	11	± 13.1	17	± 16.6	32	± 27.2	**45**	± 5
Fruticose lichen	0.5	± 0.3	1	± 0.3	**39**	± 44.5	13	± 8.9	19	± 26.3	7	± 2.9
Crustose lichen	7	± 11	11	± 7.8	35	± 41.2	**39**	± 22.5	30	± 26.2	35	± 13.2
Pleurocarpous bryophytes	0	± 0	0	± 0	**6**	± 9.4	1	± 2.2	0	± 0	0	± 0
Acrocarpous bryophytes	1	± 0.3	4	± 4.9	4	± 4.5	7	± 5.4	**19**	± 26.9	12	± 11.5
Total live cover (%)	28.5		37		102		102.5		**115.5**		102	
Mean Canopy height (cm)												
Mean shrub layer height	0	± 0	0	± 0	0.5	± 1	1	± 1.1	2	± 4	**3**	± 2.9
Mean herb layer height	0	± 0	2	± 2.9	3	± 6	3	± 1.6	3	± 3.6	**5**	± 8.7
Mean live cryptogam layer height	1	± 0.3	2	± 1.7	2	± 0.8	2	± 1.0	2	± 0.6	1	± 0

Table A2. Percent cover and mean canopy heights of plant growth forms measured on each glacial surface **fine-grain substrates**. Values in bold are the highest cover value or canopy height for a given growth form. Canopy height was measured in centimeters and cover percentages were estimated.

Fine grain Average Percent Live Cover												
	ELIA	St. Dev.	**NEO**	St. Dev.	**ITKII-AP**	St. Dev	**ITKII-N**	St. Dev	**ITKI**	St. Dev	**SAG**	St. Dev
Evergreen shrubs	0	± 0	0	± 0	0	± 0	5	± 10.4	**40**	± 12	30	± 14.5
Deciduous shrubs	1	± 0.3	1	± 0.6	0.5	± 0.3	5	± 10.1	**40**	± 12	30	± 14.8
Erect forbs	1	± 0	**3**	± 3.8	1	± 0.6	2	± 2.3	2	± 0	1	± 0
Mat and cushion forbs	0	± 0	2	± 4.0	0.5	± 0.6	**42**	± 39.7	1	± 0	1	± 0.6
Total graminoids	0	± 0	0.5	± 0	5	± 5.5	2	± 2.1	3	± 1	**40**	± 11.5
Seedless vascular plants	0	± 0	0	± 0	0	± 0	**0.5**	± 0	0	± 0	0	± 0
Foliose lichen	0.5	± 0	1	± 1.4	14	± 13.1	10	± 16.6	**15**	± 27.2	10	± 5
Fruticose lichen	1	± 0.3	2	± 1.5	10	± 6	6	± 11	44	± 4.6	**60**	± 16.1
Crustose lichen	0.5	± 0.3	15	± 24.5	20	± 27.5	11	± 0.6	**35**	± 19.8	0.5	± 0.3
Pleurocarpous bryophytes	0	± 0	0	± 0	**8**	± 0.8	4	± 8.7	1	± 0.6	0	± 0
Acrocarpous bryophytes	4	± 3.8	24	± 21.5	13	± 11.5	7	± 4	40	± 17.6	**75**	± 12.6
Biological soil crust	0.5	± 0	**14.5**	± 24.7	0.5	± 0.3	0.5	± 1.2	0.5	± 0.3	0	± 0
Total live cover (%)	8.5	± 0	63	± 0	72.5	± 0	95	± 0	221.5	± 0	**247**	± 0
Mean Canopy height (cm)												
Mean shrub layer height	7	± 4	0	± 0	0.5	± 1.2	7	± 2.6	2	± 2.0	7	± 7.2
Mean herb layer height	**10**	± 1	5	± 1.3	3	± 1.5	3	± 1.1	3	± 1.3	7	± 1.2
Mean live cryptogam layer height	1	± 0	1	± 0.6	**1.5**	± 0.6	1	± 0.8	1	± 0.6	1	± 0.6

Appendix E: Environmental Correlations

Pearson and Kendall Correlations with Ordination Axes N= 42

Axis:	**1**			**2**			**3**		
Environmental factor	**r**	**r-sq**	**tau**	**r**	**r-sq**	**tau**	**r**	**r-sq**	**tau**
Total lichen live	-0.226	0.051	-0.101	0.59	0.348	0.459	0.035	0.001	0.089
Foliose alive	0.064	0.004	0.013	0.472	0.223	0.398	-0.082	0.007	-0.043
Crustose dead	-0.05	0.002	0.07	0.401	0.161	0.258	-0.054	0.003	-0.05
Rock cover	0.552	0.305	0.353	0.2	0.04	0.238	-0.122	0.015	-0.054
Microrelief	0.098	0.01	0.079	0.315	0.099	0.206	-0.111	0.012	-0.108
Water cover	-0.068	0.005	-0.053	0.163	0.027	0.191	-0.071	0.005	-0.099
Total lichen dead	-0.3	0.09	-0.255	0.158	0.025	0.105	-0.07	0.005	-0.07
Latitude	-0.747	0.558	-0.534	0.19	0.036	0.085	-0.45	0.203	-0.31
Fruticose alive	-0.378	0.143	-0.493	0.153	0.023	0.083	0.17	0.029	0.169
Crustose alive	-0.456	0.208	-0.361	0.058	0.003	0.036	-0.074	0.005	-0.049
Longitude	0.419	0.175	0.12	-0.037	0.001	0.031	0.642	0.412	0.338
Seedless vascular plants dead	-0.1	0.01	-0.068	0.037	0.001	0.025	-0.391	0.153	-0.249
Slope (°)	0.546	0.298	0.37	0.024	0.001	0.024	-0.108	0.012	-0.076
Erect dwarf shrubs alive	-0.235	0.055	-0.218	0.021	0	-0.005	0.138	0.019	0.165
Mean low shrub layer height	-0.101	0.01	-0.027	-0.002	0	-0.011	0.082	0.007	0.08
Foliose dead	-0.456	0.208	-0.402	0.004	0	-0.014	-0.222	0.049	-0.208
Fruticose dead	-0.456	0.208	-0.402	0.004	0	-0.014	-0.222	0.049	-0.208
Pleurocarpous bryophytes dead	-0.138	0.019	-0.15	-0.04	0.002	-0.027	0.289	0.084	0.14
Elevation	0.807	0.65	0.578	-0.226	0.051	-0.028	0.407	0.165	0.285
Acrocarpous bryophytes dead	-0.33	0.109	-0.313	0.045	0.002	-0.059	0.097	0.009	0.045
Total graminoid alive	-0.327	0.107	-0.615	0.024	0.001	-0.066	0.321	0.103	0.013
Evergreen shrubs dead	-0.459	0.211	-0.536	-0.031	0.001	-0.066	0.047	0.002	-0.021
Aspect	-0.107	0.011	-0.111	-0.057	0.003	-0.073	0.239	0.057	0.159
Acrocarpous bryophytes alive	-0.455	0.207	-0.425	-0.057	0.003	-0.079	0.409	0.167	0.2
Evergreen shrubs alive	-0.552	0.305	-0.585	-0.012	0	-0.105	0.034	0.001	0.016
% clay	-0.528	0.279	-0.45	-0.067	0.004	-0.116	-0.009	0	0.056

Pleurocarpous bryophytes alive	-0.345	0.119	-0.332	-0.089	0.008	-0.121	0.015	0	-0.006
% sand	-0.496	0.246	-0.381	-0.093	0.009	-0.135	0.167	0.028	0.095
Algae alive	-0.009	0	0.037	-0.12	0.014	-0.144	0.096	0.009	0.133
% silt	-0.49	0.24	-0.43	-0.079	0.006	-0.145	-0.15	0.023	0.002
Prostrate dwarf shrubs alive	-0.497	0.247	-0.49	-0.061	0.004	-0.148	-0.036	0.001	-0.07
Erect dwarf shrubs dead	-0.232	0.054	-0.049	0.016	0	-0.148	0.139	0.019	0.11
Mean canopy height	-0.196	0.038	-0.35	-0.241	0.058	-0.151	0.141	0.02	0.082
Total graminoid dead	-0.437	0.191	-0.559	0.021	0	-0.152	0.28	0.078	0.092
Seedless vascular plants alive	-0.181	0.033	-0.165	-0.19	0.036	-0.165	-0.265	0.07	-0.197
Biologic soil crust alive	-0.284	0.08	-0.255	-0.116	0.014	-0.167	0.12	0.014	0.079
Mat and cushion forbs alive	-0.308	0.095	-0.409	-0.074	0.005	-0.179	-0.535	0.287	-0.42
% gravimetric moisture	-0.313	0.098	-0.297	0	0	-0.196	0.051	0.003	-0.049
Mat and cushion forbs dead	-0.293	0.086	-0.402	-0.056	0.003	-0.226	-0.504	0.254	-0.204
Prostrate dwarf shrubs dead	-0.423	0.179	-0.475	-0.053	0.003	-0.227	0.041	0.002	-0.083
Deciduous shrubs dead	-0.415	0.172	-0.396	-0.198	0.039	-0.231	-0.106	0.011	-0.107
Mean shrub cover	-0.26	0.067	-0.369	-0.251	0.063	-0.24	0.008	0	-0.111
Deciduous shrubs alive	-0.446	0.198	-0.434	-0.056	0.003	-0.257	0.074	0.005	-0.013
Mean dwarf shrub layer height	-0.286	0.082	-0.377	-0.276	0.076	-0.281	0.036	0.001	-0.052
% gravel	0.081	0.007	0.001	-0.339	0.115	-0.338	-0.056	0.003	-0.062
Mean herb layer height	-0.118	0.014	-0.172	-0.418	0.175	-0.375	0.234	0.055	0.119
Erect forbs alive	-0.536	0.288	-0.511	-0.352	0.124	-0.379	-0.194	0.038	-0.14
Erect forbs dead	-0.141	0.02	-0.325	-0.369	0.136	-0.414	0.227	0.052	0.105
soil pH	0.211	0.045	0.127	-0.552	0.305	-0.421	0.093	0.009	-0.009
Bare soil	-0.122	0.015	-0.209	-0.401	0.161	-0.426	-0.305	0.093	-0.162
Biologic soil crust dead	0.035	0.001	-0.076	-0.193	0.037	-0.435	0.144	0.021	0.069